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## Effects of Social and Non-Social Interpretations of Complex Images on Human Eye Movement and Brain Activation

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# **Effects of Social and Non-Social Interpretations of Complex Images on Human Eye Movement and Brain Activation**

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**Dissertation submitted to the  
School of Medicine  
at West Virginia University  
in partial fulfillment of the requirements  
for the degree of**

**Doctor of Philosophy  
in  
Neuroscience**

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## **ABSTRACT**

### **Effects of Social and Non-Social Interpretations of Complex Images on Human Eye Movement and Brain Activation**

**Amy L. Prostko**

Communicating and interacting with others is an essential part of our daily routines as humans. Performing these actions appropriately requires the ability to identify, extract, and process salient social cues from the environment. The subsequent application of such knowledge is important for inferring and predicting the behavior of other people. The eyes and brain must work together to fixate and process only the most critical social signals within a scene while passing over and / or completely ignoring other aspects of the scene. While brain activation to isolated presentations of objects and people presentations have been characterized, information about the brain's activation patterns to more comprehensive scenes containing multiple categories of information is limited. Furthermore, little is known about how different interpretations of a scene might alter how that scene is viewed or how the brain responds to that scene. Therefore, the studies presented herein used a combination of infrared eye tracking and functional magnetic resonance imaging techniques to investigate the eye movement and brain activation patterns to socially- and non-socially-relevant interpretations of the same set of complex stimuli. Eye tracking data showed that each gaze pattern was consistent with viewing and attending to only one category of information (people *or* objects) despite both categories being present in all images. Functional magnetic resonance imaging revealed that a region of the right superior temporal sulcus was selectively activated by the social condition compared to the non-social condition, an area known for its role in social tasks. Brain activation in response to the non-social condition was located in many of the same regions associated with the recognition and processing of visual objects presented in isolation. Taken together, these results demonstrate that in healthy adults, eye movement and brain activation patterns to identical scenes change markedly as a function of attentional focus and interpretation intention. Utilizing realistic and complex stimuli to study the eye gaze and neural activation patterns associated with processing social versus non-social information in the healthy brain is an important step towards understanding the deficits present in individuals with social cognition disorders like autism and schizophrenia.

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## Abbreviations

|      |                                       |
|------|---------------------------------------|
| AOI  | area of interest                      |
| ASD  | autism spectrum disorder              |
| BOLD | blood-oxygen-level-dependent          |
| FFA  | fusiform face area                    |
| fMRI | functional magnetic resonance imaging |
| FOV  | field of view                         |
| FWHM | full-width at half-maximum            |
| IFG  | inferior frontal gyrus                |
| IPL  | inferior parietal lobule              |
| LOC  | lateral occipital complex             |
| M    | mean(s)                               |
| mm   | millimeter(s)                         |
| MPFC | medial prefrontal cortex              |
| ms   | millisecond(s)                        |
| MTG  | middle temporal gyrus                 |
| PPA  | parahippocampal place area            |
| ROI  | region of interest                    |
| s    | second(s)                             |
| SE   | standard error(s)                     |
| SPGR | spoiled gradient recall               |
| STS  | superior temporal sulcus              |
| TAT  | Thematic Apperception Test            |
| TE   | echo time                             |
| TR   | scan repeat time                      |

## **CHAPTER 1: Introduction and Literature Review**

As social animals, humans are constantly required to make sense of and react to the behavior of others. Social interaction and behavior in humans involves the ability to correctly identify and process social signals and apply this knowledge in a flexible manner to produce an appropriate response. Although verbal communication provides some of the necessary information, non-verbal cues are important as well, such as facial expressions, body posture, and understanding the intentions of others. The entirety of our environment however is not socially relevant; therefore, the ability to extract socially salient information from a complex environment comprised of a variety of object categories is essential. Accomplishing this successfully requires directing our eye movements, attention, and consequent brain activity to the locations that are most likely to provide the necessary information for understanding a social interaction, while ignoring other less informative areas. This introduction discusses how humans view, recognize, and processes visual information from the environment, both non-social and social, including the object recognition, person perception and the eye movements associated with each. A section briefly covering disorders of social cognition is also included. The background information presented here will provide a foundation for understanding the experiments covered in later chapters.

## **1.1 Non-Social Object Processing**

Humans are able to easily recognize an object within a fraction of a second. Clearly, the human brain has evolved systems permitting the efficient detection, identification, and categorization of objects. The results of neuroanatomical, electrophysiological, and lesion studies in monkeys and humans show that primate vision is a highly complex process involving the interconnection of billions of neurons, which span across a multitude of visual and nonvisual brain areas. In a simplified description of the visual system, visual information proceeds from the eye to early visual areas of the brain (e.g. striate [V1] and extrastriate) that are responsible for low-level extraction of object features, such as contours and boundaries (von der Heydt et al., 1984; Livingstone and Hubel, 1988; Gallant et al., 1993; Zhou et al., 2000). From there, two information-processing streams can be distinguished, the dorsal pathway dorsal stream, which projects to the parietal cortex, is concerned with the location of objects in space, particularly for

guiding our movements in relation to those objects, whereas the ventral stream, which connects to temporal cortex, plays a role in object recognition (Ungerleider and Mishkin, 1982; Mishkin et al., 1983; Goodale and Milner, 1992). As information progresses hierarchically through these streams, receptive field sizes increase along with the ability of these areas to process increasingly more complex features of stimuli, like motion (Desimone et al., 1985; Maunsell and Newsome, 1987). Higher level stages send information from visual areas to nonvisual areas such as the prefrontal cortex and hippocampus for object related decision making and consolidating object information to memory, which can aid in the comparison of new visual stimuli to stored representations of previously seen objects, thus increasing the speed of recognition (Grill-Spector, 2003; Blumberg and Kreiman, 2010). The following sections will mainly discuss these higher order stages, particularly the regions that are part of the ventral stream, and their roles in *non-social* object and scene recognition in humans. However, much of the research on object processing involves the comparison of non-social objects to faces, thus the location of regions responding to faces as they relate to these other regions will briefly be covered. A more thorough discussion of face processing is presented in Section 1.2.1.

### **1.1.1 Generalized Object Recognition in the Lateral Occipital Complex**

Humans are able to recognize a vast array of objects, an ability that currently cannot be matched even by computers. Accordingly, object selective regions collectively referred to as the lateral occipital complex (LOC), have been identified along the human ventral stream. The LOC can be divided into a posterior region, referred to as LO, and a ventral region that overlaps the occipitotemporal sulcus and the posterior part of fusiform gyrus (Figure 1-1). Using functional magnetic resonance imaging (fMRI), a neuroimaging technique that can map brain activity by identifying changes in blood-oxygen-level-dependent (BOLD) contrast levels, studies have been able to characterize the response features of LOC. For instance, research indicates that while earlier visual areas respond similarly to both intact and scrambled pictures, the LOC is highly sensitive to pictures of intact objects compared to textures, visual noise, or scrambled images, with the magnitude of the response being similar for both familiar and unfamiliar objects (Malach et al., 1995; Kanwisher et al., 1996; Grill-Spector et al., 1998b; Grill-Spector and Malach, 2001). The stronger response to intact objects has been shown to occur not just when

passively viewing photographs but also when viewing line drawings of objects versus scrambled line drawings (Kanwisher et al., 1996). Further, activity in LOC does not seem to be affected by changes in object size or location within the visual field, and responds to an object defined by different visual cues such as luminance, texture, and motion (Malach et al., 1995; Grill-Spector et al., 1998a; Tootell et al., 1998). Electrophysiological recordings in this area using electrodes placed directly on the cortical surface of surgical patients demonstrated event-related potentials that were stronger for objects (cars, flowers, butterflies), than for scrambled control stimuli, and additionally localized regions responsive to faces and letters (Allison et al., 1994b; Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). These findings and others provide evidence that LOC is important in representing higher level object shapes rather than individual physical properties or local features of an object (Grill-Spector et al., 2001; Kourtzi and Kanwisher, 2001). The LOC also responds to presentations of multiple objects, and does not distinguish between different spatial configurations of those objects, supporting the idea that LOC encodes object identity regardless of object location (Macevoy and Epstein, 2009).

The LOC's responsiveness to pictures of objects suggests this area is important for object recognition; however, this activity could be due to other factors such as attention or arousal. Arguing against attentional and arousal factors and in favor of LOC in object recognition are studies investigating lesions of the fusiform and occipitotemporal junction, which found that damage to these areas is associated with a host of object recognition deficits (e.g. Farah et al., 1989; Damasio, 1990; Damasio et al., 1990; Moscovitch et al., 1997). In addition, disruption of recognition processes occurs when using electric stimulation (Halgren et al., 1985; Puce et al., 1999) and repetitive transcranial stimulation (Stewart et al., 2001) on these regions. Activity in LOC also increases when participants recognize images which they had been trained on, compared to untrained images presented for the same amount of time, suggesting a correlation between recognition performance and activation of object selective LOC (Grill-Spector et al., 2000).

Though much remains to be elucidated regarding the properties of brain regions for human object recognition, given its universal response to different perspectives and locations of a wide range of two- and three-dimensional objects, LOC appears to be the brain's general-purpose mechanism for perceiving the form and identity of visually presented objects (Grill-Spector et al., 2001; Macevoy and Epstein, 2009).

### 1.1.2 Category Selective Regions

In contrast to the LOC, which generally responds to any type of visual object, cortical regions in close proximity to LOC respond preferentially to images of certain types of objects. One area in medial occipitotemporal cortex, specifically posterior parahippocampal cortex, seems to respond selectively to the geometric structure of scenes (compared to faces or objects) and has thus been dubbed the parahippocampal place area (PPA; Figure 1-1) (Epstein and Kanwisher, 1998). A ‘scene’ as defined by Henderson and Hollingworth (1999) is a ‘semantically coherent (and often nameable) view of a real-world environment comprising background elements and multiple discrete objects arranged in a spatially licensed manner’. Moreover, a scene should be semantically coherent (i.e. have a ‘gist’), show aspects of a real-world environment, and contain background elements (e.g. walls) and objects that are organized in a meaningful way relative to each other (Henderson and Hollingworth, 1999). The high response for photographs of indoor and outdoor scenes is not due to low-level differences (e.g. texture, luminance), since the activation remained even after subtracting the response to scrambled versions of scenes (Epstein and Kanwisher, 1998). Other studies show a role of PPA in navigation tasks compared to control tasks that did not require navigation (Aguirre et al., 1996; Maguire et al., 1997). Together, these findings suggest that the PPA is important for processing information about the local scene, potentially for navigational purposes (Epstein and Kanwisher, 1998).

More specifically, the PPA plays a role in processing the spatial structure of the local environment, as its response increases to photographs of furnished and empty rooms but not to photographs of furniture arrays on a white background. These results indicate that the PPA activation depends on the geometry of a three-dimensional space as defined by background structures, whereas individual objects in a space have no affect on PPA activity (Epstein and Kanwisher, 1998). Additionally, the PPA responds to different types of scenes, including desktops (Epstein et al., 2003), and scenes constructed from Lego (Epstein et al., 1999), all of which convey spatial information regarding the geometry of a scene. The important component for PPA seems to be scene coherence, as responses to images of rooms that had been fractured

into component surfaces and rearranged were significantly lower than responses to fractured images that maintained the overall layout of a room (Epstein and Kanwisher, 1998).

The PPA has also been described as a ‘building’ area because it activates more to buildings than to other objects (but less to buildings than scenes) (Aguirre et al., 1998; Ishai et al., 1999). However, Epstein (2005) proposes that this description is not entirely accurate and might be due to the ambiguous nature of buildings, as they lie somewhere in between being an object and a scene. Activation in PPA to buildings may be driven by the fact that they are stable objects that are important for defining the spatial structure of the environment. Increased PPA activity to presentations of familiar buildings separate from a scene supports this idea (Epstein et al., 1999), indicating that when we are familiar with an area, we are more likely to process a building as a partial scene because it acts as a landmark that tells us something about the geometry of the surrounding space (Epstein, 2005). Interestingly, behavioral data in rats show that these animals only use objects as a landmark if they deem them to be stable over time (Biegler and Morris, 1993).

In sum, the PPA is an area that shows selectivity to images of scenes. Through its anatomical connections with other regions in the ventral stream and the parietal cortex, the PPA may aid in combining information about the location and shape of an environment (Epstein, 2005). Other connections between the parietal cortex and the hippocampus imply the PPA is likely important for representing navigationally relevant spatial information (Burgess et al., 2001). Little is known however, about the PPA’s part in processing scene gist. One study has shown that PPA activity is higher to objects that are strongly associated with a particular context than to random objects, indicating a potential role for the PPA in processing scene gist (Bar and Aminoff, 2003).

Regions demonstrating category selective activation to animals have also been reported (Martin et al., 1996). Reading the names and answering questions about the written names of animals activates the inferior region of the occipital lobe, lateral fusiform gyrus, and left superior temporal sulcus (STS). This area in the right lateral fusiform gyrus is also activated by saying the name of an animal in response to viewing a picture of that animal, indicating this area’s importance for distinguishing animals based on form (Chao et al., 1999b). In addition to animals, this same group found regions that preferentially responded to tools. Activity to naming pictures of tools and to reading the written names and questions about tools was observed in the medial



fusiform gyrus and the left middle temporal gyrus (MTG). The authors suggest that these results support a distributed network for storing object knowledge and that this network is represented within the sensory and motor systems that are active when the object knowledge is acquired (Martin et al., 1996; Martin, 1998; Chao et al., 1999b).

Further evidence for category selective regions comes from individuals with brain lesions who show selective impairment of conceptual knowledge of one category of objects compared to other categories (Warrington and McCarthy, 1983; Warrington and Shallice, 1984; Warrington and McCarthy, 1987). The categories that are most frequently disproportionately impaired or spared are ‘animals’, ‘fruit / vegetables’, and ‘artifacts’ (Caramazza and Mahon, 2003). In addition, neuroimaging studies have shown category selective responses to letter strings (Allison et al., 1994a; Hasson et al., 2002), faces (Puce et al., 1996; Kanwisher et al., 1997; Haxby et al., 2000a), and bodies (Downing et al., 2001; Peelen and Downing, 2005; Schwarzlose et al., 2005) (see Section 1.2 for more on face- and body-selective regions). Whether these regions are modules specialized for each object category separate from more generalized recognition regions (Kanwisher et al., 1997; Epstein and Kanwisher, 1998; Kanwisher, 2000; Downing et al., 2001), or are areas where recognition occurs on an individual level (e.g. due to expertise) rather than at a category level (Gauthier et al., 1999; Gauthier et al., 2000; Tarr and Gauthier, 2000), is an ongoing debate. Yet another possibility is that objects are represented by distinct patterns of responses spanning the ventral cortex, and that recognition depends on this distributed activation (Haxby et al., 2001). More research is needed to fully determine the nature of object representations in the ventral visual pathway.

### **1.1.3 Semantic Memory of Objects**

Semantic memory is one of our most defining human traits and refers to all the declarative knowledge we acquire about the world, such as the origin and history of objects, actions, and beliefs, as well as their associated meanings (Binder and Desai, 2011). The present section however, will address the neuroanatomy of semantic memory for objects and their properties. There are several theories as to how object meaning might be stored in the brain. Sensory motor property models suggest object knowledge is organized by the sensory features (e.g. form, motion) and motor properties (how an object is used), as well as potentially other

helpful functional and verbal properties (e.g. where an object might be found) related to that object (e.g. Warrington and Shallice, 1984; Warrington and McCarthy, 1987; Humphreys and Forde, 2001). Domain-specific models, on the other hand, advocate that evolutionary history, rather than sensory or motor systems, is the basis for how object knowledge is organized in the brain. In this model, dedicated neural systems are believed to exist for solving complex problems related to our survival (Caramazza and Shelton, 1998; Mahon and Caramazza, 2003). Others propose that semantic memory consists of both modality-specific representations, for example action concepts being stored in brain regions involved in planning and executing actions (a theory known as 'embodied' or 'grounded' cognition), as well as 'supramodal' representations, or combinations of attributes from different sensory modalities, such as the auditory and visual properties of an object (Barsalou, 2008; Binder and Desai, 2011). While the exact nature of concept representations in the brain is still unknown, it is likely that aspects from all of these strategies are involved.

Perhaps more important than how, is where objects information is stored. Lesion studies, neuroimaging, and other techniques suggest key roles for left ventrolateral prefrontal cortex (in particular left inferior frontal gyrus; IFG) and the ventral and lateral regions of posterior temporal cortex (see Martin, 2001; Martin and Chao, 2001; Bookheimer, 2002; Thompson-Schill, 2003; Martin, 2007). These two areas consistently activate during semantically relevant tasks, regardless of modality, attribute, or category, including semantic processing tasks of pictures and words (Vandenberghe et al., 1996b), action and color generation (Martin et al., 1995), and when naming pictures of animals and tools (Martin et al., 1996). Activity in left prefrontal cortex has also been observed in studies of semantic classification (Kapur et al., 1994; Demb et al., 1995; Gabrieli et al., 1996) and semantic monitoring (Démonet et al., 1992). Taken together, the results of these studies indicate that the left prefrontal cortex is strongly linked with top-down control of semantic memory, acting to guide retrieval and selection of conceptual information from posterior temporal and other areas of the brain (Gold et al., 2005; Thompson-Schill et al., 2005). The ventrolateral prefrontal cortex may actually be divided into two distinct areas, one for retrieval, and one for selection of the appropriate representation from among other alternatives (Badre et al., 2005). Despite debates as to the IFG's semantic specificity, this area seems to serve as an all-purpose selection system that may aid, but not be required, in semantic retrieval (Thompson-Schill, 2003; Thompson-Schill et al., 2005). Further, the prefrontal cortex is

important for providing flexible responses that are sensitive to task context (Cohen and Servan-Schreiber, 1992).

Like IFG, posterior ventral temporal cortex (including the left fusiform gyrus) activation is associated with many semantic processing tasks, irrespective of stimulus modality (auditory, visual) and format (pictures, words). Unlike IFG, the ventral temporal region is not sensitive to selection demands, but is sensitive to retrieval demands (Thompson-Schill et al., 1999), thus making the ventral temporal region key for the storage and retrieval of semantic knowledge. As described in the previous section, the ventral region of the posterior temporal lobes appears to be organized into clusters of object selective areas (Chao et al., 1999b). Activity in these clusters, especially the left fusiform, pertains to conceptual and / or lexical processes rather than to stimulus features (e.g. shape) per se. In support of this are studies showing repetition suppression in left fusiform for previously seen objects and for different exemplars of previously seen objects, in contrast to area LO, where repetition suppression was found only for previously seen objects. Since different exemplars can have different shapes while still being related, the repetition suppression in left fusiform points to an ability of this area to represent the meaning of objects as well as identity (Koutstaal et al., 2001; Simons et al., 2003).

While activity in the posterior ventral temporal cortex is elicited during conceptual processing, the posterior lateral temporal cortex activates during object property tasks, specifically those involving actions. For example when instructed to view either an achromatic object picture or a written name of an object and generate either an action or color corresponding to that object, the generation of action words produced activity in a region of posterior lateral MTG (Martin et al., 1995). This locus of activation was very close in proximity to the primary visual motion processing area. Other studies using pictures of objects whose names can refer to either the physical object itself or to the action of using that object (e.g. comb, saw), showed larger increases in left posterior MTG activity to generating the name of the action versus naming the object (Tranel et al., 2005). Additionally, activation in posterior MTG has been observed in tasks requiring semantic judgments about actions depicted in static pictures (Kable et al., 2002), and when imagining or viewing semantically meaningful actions (Decety et al., 1997; Ruby and Decety, 2001). Interestingly, these motion related responses may be category selective rather than generalized, since left posterior MTG activity is larger when naming and viewing tools compared to naming and viewing animals (Chao et al., 1999b), and when naming

tool sounds relative to animal sounds (Lewis et al., 2005; Lewis, 2006). Even though both tools and animals can move, posterior MTG seems to preferentially respond to rigid, unarticulated motion, produced when using manmade objects, rather than to more flexible, biologically relevant, motion (Beauchamp et al., 2002; Beauchamp and Martin, 2007). Using common tools additionally recruits the left intraparietal sulcus and premotor cortex, regions that are associated with the storage of visual form and action information (Martin, 2007).

Other areas have reported in semantic processing of objects, although to a lesser extent. Parietal activation has been identified when participants are instructed to make judgments about object size compared to judgments about color or sound. A potential explanation for medial parietal involvement is that our knowledge of size may partially rely on location and spatial information, hence recruitment of the parietal cortex, a key player in understanding spatial relationships (Kellenbach et al., 2001). The right middle frontal gyrus is reportedly engaged in tasks requiring flexible manipulation of stored information (Vandenberghe et al., 1996a). In addition, food related objects induce activity in systems involved in taste perception, reward, and affective response (Killgore et al., 2003; Simmons et al., 2005).

The nature of how and where object concepts are represented in the human brain is a complicated and not well-understood topic. Many questions remain regarding the development of semantic memory and the roles language or experience might play within this system. At present however, although nowhere near exhaustive, the evidence provided above argues against a unitary, amodal, undifferentiated system for representing semantic memory. Instead, object meaning appears to be distributed across several regions that are functionally and anatomically distinct, with feature selective systems being tied to certain sensorimotor modalities, and perhaps even to a particular aspect of that modality. Notably, these concept representations are often stored in the same processing streams that were active during acquisition of that knowledge (Thompson-Schill, 2003) (but see Smith and Medin, 1981).

## **1.2 Person Perception**

People, including faces and bodies represent a special category of objects because of the important meaning they have for us as a species. Therefore, the human brain has evolved dedicated neural circuits for processing person related knowledge that are separate from those for processing other classes of objects (e.g. Mitchell et al., 2002; Mason et al., 2004), but see (Gauthier et al., 1999; Gauthier et al., 2000). The following sections describe the different regions implicated in person perception, including those for faces, bodies, and the understanding of more complex social scenes and behavior.

### **1.2.1 Faces, Face Parts and Facial Expressions**

In any social situation, it is important to gather information related to the identity of an individual as well as their emotional state, thoughts, and intentions. To do this we must look for cues, many of which can be found in what has been called the ‘fundamental social stimulus’: the face (Klein and Kihlstrom, 1998). Indeed, research shows that humans are experts in analyzing faces and can quickly and precisely identify and interpret facial characteristics, particularly emotional expressions (Ekman et al., 1969; Ekman and Friesen, 1975; Bruce, 1990). A century’s worth of research in several scientific areas including developmental, behavioral, and cognitive psychology demonstrate that faces are ‘special’ and processed differently by the brain than other objects (see Nelson, 2001). This differential processing of faces is present in early childhood and becomes more refined with age (Challamel, 1992; Taylor et al., 1999). An understanding of the visual structure of faces is present even at birth, as evidenced by newborns’ preference for images of intact facial features versus scrambled or blank head-shaped stimuli (Goren et al., 1975; Morton and Johnson, 1991) and for face-like versus non-face stimuli (Valenza et al., 1996). Together, these studies support the notion of an innate ability to recognize faces.

Although some aspects of recognizing and processing facial cues may be innate, our expertise in identifying, reading, and responding to faces comes largely from experience. Information gained because of new experiences will, over time, tune and refine our face processing mechanisms. For example, human babies are born with the ability to recognize a large number of faces, including those of other species (e.g. monkeys). However, after approximately

10 months of exposure to only human faces this ability is lost, emphasizing the important role our surrounding environment plays in the development of our response to faces (Pascalis et al., 2002).

When reading faces, much of the information for determining a person's affective state or intentions can be gained from viewing the shape and configuration of individual face parts, particularly the eyes and mouth. For example, if we see a face with eyes that are slightly closed in a squint and a mouth with turned up corners, we would conclude that the person is happy. Wider eyes and a mouth pulled back into a grimace however, signifies fear. The seven basic emotions of happiness, fear, surprise, disgust, sadness, contempt, and anger are produced and recognized similarly in cultures around the world (Ekman et al., 1969; Ekman and Friesen, 1976). Perceiving emotional signals accurately is critical because they influence how we approach and remember people and help guide our interpersonal exchanges and behavior (Vuilleumier and Pourtois, 2007).

Signals of particular importance include changes in eye shape and iris / pupil position, since they can indicate another person's affective state and gaze direction. Detecting and interpreting another person's gaze has become an important adaptive behavior, alerting the observer to a potentially threatening change in the environment. Eye-gaze detection also plays an essential role in social cognition and in daily social encounters by enabling the observer to attribute affective and mental states to others and thus better understand and identify with those emotions and intentions (Dennett, 1978; Ekman, 1982; Dennett, 1987; Baron-Cohen, 1994, 1995). Without information from the eyes, discriminating between emotions becomes difficult. For example, a study by Leppänen and colleagues (2008) demonstrated that subjects were unable to discriminate between a neutral or fearful facial expression when the eyes and eyebrows within a whole face were covered. Such findings indicate the eye region alone provides much of the useful diagnostic information for the recognition of facial expressions (Schyns et al., 2007; Leppänen et al., 2008). Detecting changes in eye gaze also signals us to align our gaze in the same direction. The interaction between two people regarding a third object, known as joint or triadic attention, is thought to be one of the earliest signs of an implicit theory of mind and is apparent in humans by the age of 18 months (Blakemore and Frith, 2004). Gaze shifts then go on to trigger attentional shifts, ensuring we are aware of the actions and intentions of others and ready to react if necessary (Ristic et al., 2002; Downing et al., 2004; Nuku and Bekkering, 2008).

Most emotions not only have distinguishing eye characteristics but mouth characteristics as well. An empty open mouth defines the emotional expression of surprise and is critical for separating it from the expression of fear, since both are associated with large, widened eyes (Smith et al., 2005). An open mouth with teeth, on the other hand, is the important diagnostic feature for detecting happiness (Schyns et al., 2007). By combining information from the eyes and mouth, we are able to produce and identify a large array of emotions with minimal overlap in signals, making the human face an amazingly efficient transmitter of emotional expressions (Smith et al., 2005).

Having evolved the ability to produce a large repertoire of facial expressions suggests that we have also evolved neural systems for identifying, decoding, and processing faces and facial expressions. The idea of specialized neural mechanisms for face processing comes from studies investigating the social repercussions accompanying different types of brain lesions. For example, neuropsychological assessments of patients with bilateral occipitotemporal lesions identified an interesting change in the social behavior of these individuals: they were no longer able to recognize the faces of people they once knew (Tranel and Damasio, 1985). Patients with this type of visual agnosia, known as prosopagnosia, can describe physical features of faces but cannot name the individuals to whom they belong (Bodamer, 1947; Damasio et al., 1982). The ability to perceive other objects, however, remains intact in these individuals (Farah et al., 1995; Henke et al., 1998). These studies support the existence of separate visual processing networks for recognizing faces and objects, however there may also be separate networks for processing facial expressions. Bilateral amygdala lesions in humans impair the recognition of fearful facial expressions while leaving the recognition of face identity intact (Adolphs et al., 1994; Adolphs et al., 1995). Additionally, patients with Huntington's disease, an autosomal-dominant neurogenetic disorder that in its early stages affects regions of the basal ganglia, show a disproportionately severe deficit in recognizing facial expressions of disgust compared to other expressions (Sprengelmeyer et al., 1996). Together, such findings imply that humans have developed specific processing mechanisms for both facial identity and expression.

In addition to lesion studies, electrophysiological studies that record event-related potentials from occipitotemporal scalp electrodes have identified a peak that occurs around 170 milliseconds (ms) after the onset of a visual stimulus (e.g. Bentin et al., 1996; Jeffreys, 1996) that is sensitive to images of faces. This event-related potential, known as the N170 component,

has a larger amplitude and shorter latency to faces than to non-face objects, indicating selectivity for facial stimuli (Bentin et al., 1996; Allison et al., 1999). Although electrophysiological studies can provide information regarding the timing of brain responses (and occasionally spatial location in the case of intracranial recordings, (e.g. Allison et al., 1999)), often other techniques are necessary to elucidate the regions of the brain recruited during face processing tasks. Neuroimaging methods, including both fMRI and positron emission tomography, have indicated a region of the lateral fusiform gyrus that is especially responsive to faces compared to viewing other objects (e.g. Sergent et al., 1992; Kanwisher et al., 1997; Ishai et al., 1999). Additionally, lateral fusiform activity increases when performing face matching tasks as compared to location matching tasks (Figure 1-1 and 1-2) (Haxby et al., 1994). This region also seems to be sensitive to face stimuli, as demonstrated by an increase in activity in response to viewing intact versus scrambled faces (Puce et al., 1995; Kanwisher et al., 1997). Because of its consistent response to face stimuli, this lateral portion of the fusiform gyrus has become known as the fusiform face area (FFA). Although, there is evidence that the FFA conveys some information representing non-face objects (Chao et al., 1999a; Ishai et al., 1999; Haxby et al., 2001), especially when those objects are perceived as distinct individuals within a category rather than as nonspecific exemplars (Gauthier et al., 1999; Gauthier et al., 2000). Nonetheless, much of the reported activity in the FFA is right hemisphere biased (Puce et al., 1996; McCarthy et al., 1997), which serves to further support the idea of a separate processing pathway for faces, since the right fusiform gyrus is a major component within the ventral system for object recognition (Ungerleider and Mishkin, 1982; Merigan and Maunsell, 1993).

Face perception also involves other areas in visual extrastriate cortex, including the lateral inferior occipital gyri (occipital face area) and the posterior STS (Kanwisher et al., 1997; Puce et al., 1998; Halgren et al., 1999; Haxby et al., 1999; Hoffman and Haxby, 2000). Work by Perrett and others have identified neurons in the STS of monkeys that were responsive to face stimuli, including different gaze and head orientations (Perrett et al., 1985; Perrett et al., 1992; De Souza et al., 2005). In humans, evidence for the involvement of these areas derives from studies using temporal lobe epilepsy patients undergoing surgery, which identified face-specific responses from electrodes placed on the cortical surface of the brain in these occipitotemporal regions. More specifically, these intracranial recordings showed that cortical stimulation of the face-specific regions evoked a transient inability to name familiar faces or evoked face-related



hallucinations (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Furthermore, the posterior STS is activated when viewing static images of faces (Kanwisher et al., 1997; Chao et al., 1999b; Halgren et al., 1999; Haxby et al., 1999; Hoffman and Haxby, 2000), and also during perception of biological movements of the face, such as eye and mouth movements (Puce et al., 1998). It has been suggested that while the fusiform may be important for recognizing facial identity, the STS extracts other elements of the face, like eye gaze information and emotional expression (Haxby et al., 2001; Haxby et al., 2002). Collectively, the FFA, inferior occipital gyri (occipital face area), and STS are thought to be the core system essential for the perception of faces in humans (Figure 1-1 and 1-2) (Haxby et al., 2000a).

Once the core system performs an initial visual analysis of a face, additional regions can be recruited for increasingly detailed analyses. One key structure is the amygdala, which aids in evaluating and interpreting eye gaze (Kawashima et al., 1999) and emotional signals from the face (Adolphs, 1999; Morris et al., 2002), thus serving as a ‘relevance detector’ for meaningful events and emotional salience (Sander et al., 2003). Neuroimaging studies have shown amygdala activation to overt (Adolphs et al., 1994; Morris et al., 1996) and masked (Morris et al., 1998; Whalen et al., 1998) emotional face images, especially those that are fearful or threatening (LaBar et al., 1998; Moses et al., 2007), highlighting its importance for alerting us to potential dangers in our environment. Working in concert, the core and extended system, including the amygdala allow us to detect and read information from faces.

### **1.2.2 Bodies, Body Parts, and Bodies in Action**

Although attention to gaze direction or mouth shape is important, these cues alone may not be sufficient to understand a social situation fully. Interpreting a social scene first requires us to detect the presence of an ‘intentional actor’, which is most commonly another human body or their body parts (Saxe, 2006). From there, as noted by Darwin (1872), we can read body postures that convey valuable information about a person’s intentions and their affective responses towards objects. Like facial expressions, body language can communicate a variety of signals, and our ability to detect these signals is established within the brain at an early age (Bertenthal, 1993). One effective method for studying body signals is to attach light sources to an actor’s joints and then record body movements and postures in the dark (Johansson, 1973). With this

method, studies have found that observers can detect differences between human movement and random movement, and can also identify subtle characteristics of human movement, such as gender, personality traits, type of action (such as dancing), and emotion from a point-light series of postural configurations (Dittrich et al., 1996).

The information obtained from viewing body language can influence and add to the processing of facial expressions and emotions. Studies show that information from body expressions can help reduce ambiguity within a facial expression (van Hoof, 1962). This ability may be beneficial, for example, during a frightening event where we may not have a full view of another person's facial expression or if we are positioned too far away from others to see their facial expressions clearly. By combining facial and body signals, we gain a better understanding of the environment. Observing the emotional body expressions of others can also prepare us to engage adaptive reaction strategies, which facial information alone cannot always provide (de Gelder, 2006). For example, while a fearful face indicates threat, it does not present much information regarding the cause of the threat or the most appropriate exit strategy. A bodily expression, however, is able to both signal fear and demonstrate the flight action of that individual, thus allowing our own body to prepare for the same reaction (de Gelder et al., 2004). Because emotional body language utilizes coordinated movements of the whole body to express emotions and meaningful actions, experiments presenting stimuli containing bodies can therefore provide a more comprehensive understanding of human perception and action than studying facial expressions alone.

As for faces, the human brain likely has regions specialized for processing visual representations of bodies. Event-related potentials measured during electrophysiological studies have identified a peak called the N190 component that is sensitive to depictions of the human body including photographs, silhouettes, and stick figures, but not scrambled versions of these images (Thierry et al., 2006). Additionally, patches of ventral and lateral occipitotemporal cortex have been found that are explicitly sensitive to static images of hands (Allison et al., 1994a; McCarthy et al., 1999; Puce et al., 1999) as well as to dynamic images of hands and legs (Wheaton et al., 2001). Using fMRI, several brain regions have been identified that preferentially activate to body stimuli. Downing et al. (2001) reported greater activation in a region of the right lateral occipitotemporal cortex when participants viewed photographs of human bodies and body parts compared to viewing images of inanimate objects and object parts, and subsequently

designated this region the extrastriate body area (Figure 1-3). This area responded not only to photographs but also to line drawings, silhouettes, and stick figures of the human body and body parts, and is selective to human bodies, but not to bodies of other animals. The authors suggested that such a specialized system for processing visual depictions of the human body might aid in identifying individuals when the face is not visible, or for inferring the actions or intentions of others (Downing et al., 2001).

In addition to the extrastriate body area, an area of the fusiform gyrus also shows a preference for images of the human body (see Figure 1-3) (Peelen and Downing, 2005; Schwarzlose et al., 2005). Although there initially appeared to be significant overlap between the fusiform body area and the FFA (Peelen and Downing, 2005), further experiments have demonstrated that at high fMRI scanning resolutions, the fusiform body area is both spatially (Schwarzlose et al., 2005) and functionally (Peelen et al., 2006) dissociable from the FFA. This region is also sensitive to emotion, as demonstrated by Hadjikhani and de Gelder (2003) who found increases in activation bilaterally in the fusiform cortex in response to images of bodies expressing fear compared to neutral bodies. The fusiform and extrastriate body areas each make separate contributions to body processing. The fusiform body area shows a step-like response to torsos and headless bodies relative to smaller body parts (Taylor et al., 2007), whereas responses in the extrastriate body area are greater to intact depictions of the body compared to depictions where the torso and limbs are separated from each other in visual space, even when these depictions are partially occluded (Thompson et al., 2005). Extrastriate activity also increases proportionally with the amount of the body that is visible while still showing a high degree of selectivity even for single digits (Taylor et al., 2007). Both areas however, activate in response to sparse movement patterns of the body that invoke the percept of a person performing an action. Further, activity in both body areas is strongly correlated with the activity to biological motion, suggesting that the biological motion responses that had previously been attributed to face-selective activity in FFA and motion-selective neurons in area hMT+ (Grossman et al., 2004), is instead due to body-selective activity in the fusiform body area and extrastriate body area, respectively (Peelen et al., 2006).

Another brain region that is involved in the perception of biological movement of the human body is the STS (see Figure 1-3) (Allison et al., 2000; Grossman et al., 2000; Wheaton et al., 2001; Grossman et al., 2005; Thompson et al., 2005). While the fusiform and extrastriate

body areas are thought to respond in general to body forms without taking into consideration the type of movement (Downing et al., 2006; Peelen et al., 2006; Kontaris et al., 2009), the STS responds preferentially to movements that are biologically relevant (Beauchamp et al., 2002; Thompson et al., 2005), especially those with communicative potential and social salience (Campbell et al., 2001; Puce and Perrett, 2003; Morris et al., 2005). For instance, different parts of the STS become active when observing an emotional body expression. Fearful expressions activate both the anterior and posterior part of the right STS, while happy expressions produce increased activation in anterior STS (van de Riet et al., 2009). The sensitivity of the STS for emotional body expressions is potentially the result of its connections to the amygdala (Stefanacci and Amaral, 2000), a region which is also activated when observing body expressions, particularly expressions of fear (Hadjikhani and de Gelder, 2003; de Gelder et al., 2004; Grezes et al., 2007; van de Riet et al., 2009). Emotional modulation in body-selective areas likely improves the speed and accuracy with which we detect and recognize emotionally relevant body positions (Peelen and Downing, 2007).

Similarly, feedback among and between these and other regions is critical for perceiving human actions and deciphering intentional behavior. Importantly, the above mentioned body areas, along with regions of parietal, frontal, and premotor cortices play a role in preserving our sense of body and limb position (for a review see Peelen and Downing, 2007), or body schema (Head and Holmes, 1911). By integrating internal motor signals with external visual input, these regions act as a system for distinguishing our own body from that of another person (Astafiev et al., 2004; Jeannerod, 2004; David et al., 2007). Knowing self from other is likely central to imitation, which involves copying body movements through the observation of others (Brass et al., 2001; Brass et al., 2005; Brass and Heyes, 2005). The ability to imitate begs the question of ‘how the observer’s motor system [can] know which muscle activations will lead to the observed movement if the observer does not see the underlying muscle activation in the actor’ (Brass and Heyes, 2005)? One theory proposes that ‘mirror’ neurons, discovered in premotor area F5 and in area PF/PFG within the inferior parietal cortex of monkeys, are able to resolve this problem since this type of neuron responds both during the execution of a goal-directed action and when observing that action performed by another (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996; Gallese et al., 2002; Fogassi et al., 2005; Fogassi and Luppino, 2005). Because mirror neurons respond both when observing and executing actions, it has been

suggested that they have the potential to map observed movements onto a motor program, and thus may be important for imitation (Heyes, 2001; Rizzolatti et al., 2001; Iacoboni, 2005; Rizzolatti, 2005; Iacoboni and Dapretto, 2006; Molenberghs et al., 2009). Although direct evidence for the existence of mirror neurons in humans is lacking (see Dinstein et al., 2008; Turella et al., 2009), there is some indirect evidence suggesting that a mirror neuron system does exist in humans. fMRI studies of humans have demonstrated that there are brain areas in humans that exhibit overlapping activation for observed and executed actions (e.g. Iacoboni et al., 1999; Dinstein et al., 2007; Chong et al., 2008). In one study, observing and executing finger movements produced activation in anatomically homologous regions to those found in monkeys, namely the IFG and rostral posterior inferior parietal lobule (IPL) (Iacoboni et al., 1999). The IFG and posterior IPL, in conjunction with visual input from and feedback to the STS, are said to comprise the core imitation circuit and human mirror neuron system (Figure 1-4) (Iacoboni, 2005; Iacoboni and Dapretto, 2006). However, the exact contributions of these areas to imitation, including whether IFG is even necessary for imitation given the relatively poor imitation skills of monkeys (Whiten and Ham, 1992; Visalberghi and Frigaszy, 2001), are still controversial (Dinstein et al., 2008; Molenberghs et al., 2009).

Other theories for how humans are able to imitate the actions of other people tend to fall into one of two categories: specialist or generalist (Brass and Heyes, 2005). Specialist theories claim that imitation is mediated by a special purpose mechanism. One specialist theory, active intermodal matching, has its roots in controversial research regarding the abilities of newborn infants to imitate facial gestures and purports that the initial visual representation of a movement is converted into a ‘supramodal’ representation that contains information about ‘organ relations,’ but this theory does not specify exactly how this information might be encoded (Meltzoff and Moore, 1979; Anisfeld, 1996; Heyes, 2001; Meltzoff, 2002). Generalist theories on the other hand, assert that imitation is mediated by general learning and motor control mechanisms rather than special purpose mechanisms. The first of two main generalist theories is the ideomotor theory, which considers imitation to be part of a general motor control mechanism representing actions in the form of sensory ‘images’ that can then be used to initiate and control body movements (Greenwald, 1970; Prinz, 1997, 2002). The second generalist theory is the associative sequence learning model, which maintains that the ability to imitate is a product of general processes of associative learning that link the otherwise separate visual and

somatosensory components of an action (Heyes, 2001; Heyes and Ray, 2004). Existing evidence tends to support generalist theories; however, alternative theories for understanding imitation are still being discovered. For instance, recent studies on imitation suggest that the neural processes involved in representing observed, imagined, and imitated actions, may be dissociable, and perhaps even hierarchically organized (Macuga and Frey, 2012). Moreover, action imitation and action understanding may also be sustained by dissociable mechanisms, with imitation recruiting left frontal processes likely related to learning mechanisms, and action understanding engaging right posterior regions, further highlighting the involvement of these posterior regions in socially relevant behavior (Carmo et al., 2012). Social actions and behavior, such as social mirroring, or the non-conscious change in behavior towards mimicking the mannerisms, posture, and expressions of other individuals during a social interaction (Chartrand and Bargh, 1999), may go beyond simple imitation mechanisms, recruiting systems for emotions, empathy, and understanding the intentions and mental states of other individuals (Iacoboni, 2005; Iacoboni and Dapretto, 2006). The next section discusses how regions processing information from the face and body work together with these additional systems when viewing complex scenes and engaging in higher-order social behavior and interactions.

### **1.2.3 Complex Social Scenes and Behavior**

Cues from faces and bodies are clearly central for interpreting social and emotional information. However, in the real world, faces and bodies do not usually appear against a plain black or white background; instead, we are more likely to be surrounded by a multitude of objects and contexts. With such an innumerable variety of complex environments, important questions arise regarding methods for cue extraction from background context and the benefits background context can offer for interpreting social scenes.

When viewing complex social images, there is evidence suggesting emotional contexts can be beneficial. For one, emotional scenes, particularly threatening ones, are rapidly detected and appraised for both phylogenetically (snakes) and ontogenetically (guns) significant content (Ohman et al., 2001b; Fox et al., 2007). Similarly, threatening angry faces are detected more quickly and accurately than faces depicting other emotions such as sadness (Ohman et al., 2001a), or happiness (Krysko and Rutherford, 2009). Expressive faces and pictures likewise

activate many of the same brain regions, such as the amygdala, posterior hippocampus, ventromedial prefrontal cortex, and visual cortex (Britton et al., 2006). Since emotion affects both faces and scenes in parallel ways, how are their responses affected when emotional faces and scenes are combined? A study by Righart and de Gelder (2006) demonstrated a N170 amplitude that was more negative when a face (fearful or neutral) was presented in combination with a fearful background context. This effect did not occur when a fearful face was presented in combination with a neutral background, indicating an emotional context is able to add important information about facial expressions that can then influence how they are encoded in the brain. However, context information may not always work in our favor, as contextual framing has also been shown to mislead observers into perceiving neutral faces as happy or sad (Wallbott, 1988) or angry faces as fearful (Carroll and Russell, 1996). Misleading or not, contextual information plays an important role in social attributions because it can influence how the brain encodes and categorizes objects and people (Cox et al., 2004), as well as alter our perception of facial expressions and mental states (Mobbs et al., 2006).

These and other studies suggest that our perception of the social world relies on continually updating and integrating stored contextual experiences with contextual information extracted from our current surroundings (Bar, 2004). Hence, we must constantly monitor the actions and expressions of another person as well as the social context around them for important changes (Klin et al., 2003). This social context is not likely to contain only background objects, but more often than not will involve the presence of other people as well. Do the actions and emotions of a group of people affect how we respond to viewing a single person? A series of experiments by Kret and de Gelder (2010) found that when actions performed by people in the background are emotionally congruent with that of a central character, the recognition speed for the emotion of the central target character increased. Specifically, participant reaction times, especially those to fearful and angry scenes, were faster to presentations where the target character's body expression was congruent with the emotion of the individuals in the scene compared to presentations where the body expressions were incongruent. The results of this study highlight the influential role of emotional *and* social aspects of a scene on our perception of others (Kret and de Gelder, 2010).

To deal with the daily deluge of complex social and emotional situations, humans have developed systems that allow inherent understanding of the actions, feelings, and intentions of

other people. For instance, humans have the capacity to attribute opinions, perceptions, beliefs, and attitudes to other individuals for the purpose of predicting and explaining their behavior, a process known as mindreading (Baron-Cohen, 1995), theory of mind (Premack and Woodruff, 1978), or mentalizing (Frith et al., 1991; Frith and Frith, 1999). There are two main arguments that attempt to explain the psychological processes underlying theory of mind, the Theory Theory and the Simulation Theory. The Theory Theory suggests that a set of causal laws relating external states, internal states, and behaviors are used to construct theories about the mental states of others (but see Gopnik and Wellmann, 1992; Perner and Howes, 1992). Simulation Theory, on the other hand, proposes theory of mind arises via the process of simulating others' circumstances, or pretending to be in another's shoes, through which one can experience the another person's internal states (Harris, 1995; Stone and Davies, 1995; Gallese and Goldman, 1998). In other words, we rely on the brain's ability to link together first- and third-person experiences of action and emotion (e.g. link 'I do' with 'he feels'), thereby allowing us to use knowledge of our own feelings or action experiences to simulate how another person might feel or act in a given situation (Gallese et al., 2004). While evidence leans more towards the Simulation Theory, particularly in light of the discovery of mirror neurons, these two theories need not be mutually exclusive. For example, it is plausible that the more cognitively demanding Theory Theory may be adopted when simulation is inappropriate (Carrington and Bailey, 2009).

Mentalizing about others, at least in part, appears to use similar brain regions to those used when attributing mental states and beliefs to one's self (Vogeley et al., 2001). The brain regions that constitute the mirror neuron system may underlie some forms of simulation because of their unique 'mirror' responses to both the observation and execution of a goal-directed action. Because activity in the mirror neuron system represents a motor plan, an observer watching someone else perform an action is able to experience the observed action via the same mechanisms as the person performing the action, except that the observer's motor responses are inhibited. Mirror neuron activity therefore puts the observer into the same 'mental shoes' as the performer, at least for actions, however simulating the intentions behind the action likely involves a more complex system (Gallese and Goldman, 1998).

The cognitive mechanisms affiliated with inferring the intentions and mental states of other people are thought to be innate (Leslie, 1987; Leslie and Roth, 1993; Leslie, 1994) due to the uniformity with which they develop across cultures (Avis and Harris, 1991) with little



individual variation (Happé, 1995). By the age of four, humans are able to understand the concepts of reality and belief, and that one person's belief may or may not coincide with reality (see Frith and Frith, 2003). Tasks ranging from stories and cartoons, to animated geometric shapes and interactive games, have been used to ascertain the neural basis for mentalizing. Three main areas are thought to be important for mentalizing: medial prefrontal cortex (MPFC), temporal poles, and the posterior STS (Figure 1-5) (Frith and Frith, 2001; Frith and Frith, 2003). The MPFC refers to the anterior-most part of the anterior cingulate cortex, which has direct connections to the temporal poles and STS (Bachevalier et al., 1997). This region most frequently responds to tasks involving attending to, or making judgments about, the mental states of self or others and is proposed to play a role in signaling the decoupling between reality and beliefs (Frith and Frith, 1999; Frith and Frith, 2003). Mentalizing tasks involving semantics (Vandenberghe et al., 1996b; Noppeney and Price, 2002b, a), familiar faces and scenes (Nakamura et al., 2000), and autobiographical information (Fink et al., 1996) all activated the temporal poles. The anterior temporal poles receive input from the limbic system and are a potential site for convergence of information from all sensory modalities (Moran et al., 1987), and are thus well-suited for making use of our past experiences to provide us with a contextual framework for a given task (Frith and Frith, 2003).

Like the temporal poles, the posterior STS is a multimodal integration site with connections to the limbic system (Barnes and Pandya, 1992). Responses in this region extend beyond biological motion to more abstract representations of observed intentional actions (Saxe et al., 2004). For example, several studies report activity in posterior STS (as well as MPFC and temporal poles) when viewing animations of geometric shapes depicting social interactions compared to viewing randomly moving shapes (Castelli et al., 2000; Schultz et al., 2004). The high responsiveness of the STS to a range of tasks involving faces, bodies, scenes, emotion, and mentalizing, underscores its centrality to social perception (Gallagher and Frith, 2003; Saxe, 2006; Zilbovicius et al., 2006). Additional regions apart from the three described above have been reported in various tasks of social information processing as well, such as the temporo-parietal junction (see Frith and Frith, 1999), amygdala, and orbito-frontal cortex (Brothers, 1997). How these systems interact to extract and process social information from our complex environment is still not well understood. Human social behavior has seemingly innumerable facets, leaving much to be discovered regarding their underlying neural correlates.

## **1.3 Human Eye Movements and Perception**

Researchers from disciplines ranging from economics to computer science to medicine have aimed to discover how we view our environment, including why we look where we do and how our eye movements relate to perception. These same questions have remained relevant, from initial studies by Buswell (1935) all the way to the present day. By measuring eye movement behavior, we can gain a better understanding of both visual and cognitive processing. However, even after decades of research, much still remains unclear regarding eye movement guidance due to the many factors that can affect it, including the physical properties of a stimulus, object recognition, and goal-directed tasks (Schütz et al., 2011).

There are advantages to studying eye movements despite the difficulties. First, the number of movement types is limited, and second, eye movements are readily accessible and observable. As a result, reasonably precise and systematic examinations and interpretations of these eye movements can be obtained. Evaluating these movements involves counting the number of fixations in regions of a scene as well as their durations. Saccades made during purposeful behavior also have characteristics that can be measured, such as velocity, duration, trajectory, and latency (see Leigh and Zee, 2006). The measurements for each type of movement can be compiled to provide a visual depiction of a person's visual scan pattern during any given task. Moreover, because eye movements are often the behavioral outcome of attentional shifts, recording them provides us with a method for physically mapping attention engagement locations (Henderson, 2003). The two main types of eye movements that will be covered here are saccades and fixations, focusing mainly on visual fixations and their role in attention, as well as on how they are affected during various scene-viewing tasks.

### **1.3.1 Saccades, Fixations, and Visual Attention**

Humans acquire high quality visual information from a limited spatial region surrounding the center of gaze (the fovea), which subtends a visual angle of about two degrees. Outside the center of gaze, visual quality drops quickly into a low-resolution visual surround. Therefore, when investigating our surroundings we must continuously move our eyes via rapid eye movements called saccades, to reorient the fovea (Henderson, 2003). Javal (1879) and Landolt

(1891) were the first to use the word saccade in order to describe the rapid eye movements we make when reading and when voluntarily changing our gaze position, but the word has since come to refer to many types of voluntary and involuntary shifts of fixation, including those that occur during sleep (Zhou and King, 1997). However, object and scene information for perceptual or cognitive analysis is not acquired during a saccade phase, but rather during fixations, the periods of relative gaze stability (Matin, 1974; Volkman, 1986; Thiele et al., 2002). Consequently, vision is an active process that requires making saccades in order to direct our fixations to different scene regions.

What factors lead us to fixate on a given area? The first thorough investigation to record and analyze human eye movements to complex scenes was carried out by Buswell (1935), using an eye tracking apparatus specifically built for recording both the horizontal and vertical eye position during the course of image viewing. These early studies showed that empty, uniform, and uninformative scene regions are often not fixated, while interesting and informative regions are fixated first and more frequently (Buswell, 1935). There are several theories for what makes a region ‘interesting and informative’. One theory, points to bottom-up stimulus-based information, while another cites top-down knowledge-based information. The contribution of each of these in guiding visual search behavior has long been the topic of debate (see Egeth and Yantis, 1997 for a review). Bottom-up perspectives state that view patterns are the result of sequentially attending to areas with high discontinuities in low-level features, such as contrast, luminance, edge detection, and textures among others (Koch and Ullman, 1985; Itti and Koch, 2000). Evidence challenging the low-level saliency map model comes from reports of mismatches between model generated scan paths and human generated scan paths to real world scenes (Foulsham and Underwood, 2008). Although low-level features may explain looking behavior when encoding all aspects of a visual scene (as in a memory task), top-down influences are evident during more purposeful viewing of scenes where areas of low-level saliency are ignored if they do not contain goal-related information (Underwood and Foulsham, 2006). The ability to control gaze and attention allocation based on current needs seems the more logical method for real world tasks. For example, assessing the threat level of a person walking down an alleyway would not be possible without the ability to ignore low-level signals, like the texture of the pavement beneath our feet or the contrasts created by shadows, in lieu of focusing on the

facial expression and body posture of the approaching person. Therefore, top-down control is the more relevant perspective for the current discussion.

Integral to goal-driven gaze control is the human attention system, which serves to coordinate our actions by working to distribute limited resources among various tasks (Kahneman, 1973). This system assesses task difficulty and then allocates resources according to current priorities (Recarte and Nunes, 2000). Eye fixations are often a direct reflection of this allocation of attention (Chua et al., 2005) as indicated by research showing that visual attention and saccadic eye movements are closely linked both spatially and temporally (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996). Therefore, a change in visual inspection pattern can be interpreted as a change in the allocation of spatial attention (Kahneman, 1973; Moray, 1990, 1993). This connection between attention and visual inspection strategy helps us plan our eye movements (Henderson, 1993), either toward objects that automatically attract attention because of conspicuous or contrasting attributes, or towards locations preselected by expectations and current goals (Theeuwes, 1993, 1995). The important outcome from this link between attention and eye movements is that the areas within a scene that are frequently fixated are the regions drawing the most attention and thus deemed the most interesting by the viewer (Berlyne, 1958). Additionally, fixation durations are likely to increase when viewing the most interesting regions (Biederman et al., 1982), as well as when extracting a large amount of information from a target (Rayner and Morris, 1990). Locations that are not fixated are scarcely processed or not processed at all (Johnston and Dark, 1986; Theeuwes, 1995), emphasizing the link between fixations and visual attention which together enhance perceptual processing of a visual scene.

### **1.3.2 Effect of Task on Eye Movements**

Eye movements have been recorded during many types of activities including reading, looking at pictures, drawing, walking, playing sports, and performing goal-directed motor acts such as making tea (see Land, 2006). Most relevant to the current discussion is the act of viewing a picture. Compared to reading, where fixations are constrained, moving linearly to the right across a page (in English) in an orderly fashion, passively viewing a picture is generally less confining in regard to fixation order. However, Buswell (1935) noted that the patterns of

fixations to viewed pictures were not completely random, but at least in part reflected the structure of the presented image. One interesting observation he made was that the initial fixations directed to a picture were relatively focused and short, whereas later fixations were longer and more spread out, suggesting detailed analysis of a picture is subsequent to a brief exploratory perusal (Buswell, 1935). Other groups have replicated these findings, showing fixations to a scene can be divided into an initial survey phase, where fixation patterns tend to be similar between viewers, and a later phase, where fixations are made to regions of greater meaning or semantic interest, with a decrease in coherence between viewers (Henderson and Hollingworth, 1998; Tatler et al., 2005).

Going beyond the study of passive scene viewing, Buswell (1935) noticed that asking a participant different questions about a scene led to changes in the participant's pattern of fixations. This ability to direct our fixations through a scene in real time in the service of ongoing perceptual, cognitive, and behavioral activity, is a process known as gaze control, and implies that our eye movements are influenced and altered in ways that correspond to the nature of our current goals. Indeed, several early studies of eye movements during scene viewing demonstrated that task demands affect the resultant patterns of saccades and fixations (also referred to as gaze paths or visual scan paths / patterns) (Buswell, 1935; Yarbus, 1967). The scan paths in Figure 1-6 from a single participant (Yarbus, 1967), show that despite viewing the same image in each task, the locations and distributions of fixations within that image change depending on the underlying goal of the viewer. For instance, the patterns produced when instructed to remember the clothes worn by the people in the scene or to estimate how long the 'unexpected visitor' had been away are highly focused, with fixations and saccades directed mainly to the people's bodies and faces, respectively (Figure 1-6, B, D). In contrast, the visual scan path generated when instructed to remember the positions of the objects in the room is scattered, with fixations and saccades being widely distributed over the entire image (Figure 1-6, C). Together, these scan path recordings highlight the role of task instruction during scene viewing; the pattern of fixations points to the regions that are most relevant to a particular task, while unfixed scene regions presumably serve no helpful purpose for the given task. The initial observation by Buswell and subsequent follow-up experiments by Yarbus showing that eye movements are not simply reflexive responses to low-level features of a scene, but instead can be

triggered by top-down factors related to the demands of a task, was an instrumental discovery in the field of eye movement research (Buswell, 1935; Yarbus, 1967).

The visual input provided by a presented image works in concert with knowledge and memory systems to control our eye movements during a task. These systems utilize information gained from previously attended locations in a current scene (short-term memory), stored visual, spatial, and semantic information (long-term memory), as well as knowledge about our goals and plans, both past and present, to help us more efficiently view a scene (Henderson, 2003; Henderson and Ferreira, 2004). Through a single saccade and fixation, we are able to acquire enough information about the global gist, or gestalt, of a scene and its spatial layout to guide future fixations to regions most likely to contain a particular object (Henderson et al., 1999; Oliva et al., 2003). Evidence for the involvement of short-term knowledge recruitment during a scene viewing task comes from studies showing that semantically interesting or informative areas are often re-fixated during a viewing session (Buswell, 1935; Yarbus, 1967; Loftus and Mackworth, 1978; Henderson et al., 1999), a process that ensures fixation of highly relevant objects (Land and Hayhoe, 2001). An example of how long-term memory influences scene viewing is demonstrated by a viewer's tendency to fixate empty regions of a scene if those regions held informative value in a previous task (Henderson and Ferreira, 2004). Additionally, 'scene-schema knowledge', or the generic knowledge about a particular type of scene, including the types of objects found in different categories of scenes (e.g. kitchens are associated with stoves), can influence our gaze patterns, as does generic world knowledge (e.g. objects do not float in the air) (Mandler and Johnson, 1976; Friedman, 1979; Biederman et al., 1982; Henderson, 2003). By integrating knowledge from a variety of sources, we are able to guide our eye movements to locations in a scene that maximize information extraction based on relevancy to our current task, goal, or plan (Henderson, 2003).

### **1.3.3 Viewing Socially Relevant Images**

Previous work has shown that the human visual system is able to detect behaviorally and evolutionarily relevant objects rapidly within a complex natural scene. For example, when two natural scenes are simultaneously flashed left and right of a fixation point, participants are able to make reliable saccades to the image containing an animal as early as 120-130 ms (Kirchner and

Thorpe, 2006). These saccades are not random, but are accurately localized to the animal in an image, particularly to the head (Drewes et al., 2009; Drewes et al., 2011). The responses to such saccadic choice tasks are even faster when the image contains a human face, with saccade initiation as early as 100-110 ms after image onset (Crouzet et al., 2010). The bias toward saccading to faces is hard to suppress, as indicated by the tendency for participants to direct saccades towards faces even when instructed to make saccades to vehicles (Crouzet et al., 2010). Additionally, participants have difficulty looking away from faces when performing anti-saccade tasks (Gilchrist and Proske, 2006). It has therefore been suggested that this bias for viewing faces may be innate, since when given no instruction other than to make a saccade to one of two presented images, participants preferred to saccade towards images containing humans (Fletcher-Watson et al., 2008). The results of these studies imply a behavioral and social advantage for the detection of animals and even quicker detection of humans in a scene; such systems likely evolved to permit efficient identification of predators or food sources, as well as to separate potential friends from foes.

While quick detection of faces is important, we are unlikely to see images of people flashing briefly in front of us in places outside of the laboratory (except maybe on television). Rather, it is more realistic to investigate human eye movement during longer presentations of complex social scenes. As introduced above, Yarbus (1967) was one of the few investigators to record gaze patterns using a variety of social scenes. These scenes ranged in complexity from images of an isolated face, to the body and face of a single person, to images of the entire body and face of several interacting people. Recordings showed that, in addition to task, the type of scene itself also altered eye movement patterns. For example, when participants were presented with images of faces in isolation, their scan patterns indicated a clear preference for viewing the eye region of the face. In contrast, when both the face and body of a single individual were present, no such preference for the eyes emerged. Interestingly, when an image contained multiple people (faces and bodies), participants tended to return to focusing mainly on the faces and heads rather than other body parts (Yarbus, 1967). These different patterns raise the questions of why and when viewing the eye region(s) of a person (or people) within a scene is critical. Birmingham and colleagues (2008b) proposed two intriguing explanations. First, increasing the social content through the addition of more people to a scene enhances focus on the eye regions, or alternatively that increasing social content by not just adding people, but also

increasing the activity level of those people within a scene promotes increased viewing of the eyes. To test these hypotheses, participants were instructed to either 'look' at a series of images, 'look at and then describe' the scenes, or 'look at and then describe where attention is being directed' by the people within a scene (social attention task), while their eye movements were recorded. The scenes contained either one or three people that were either inactive or actively interacting with background objects or the two other people (if present) (Birmingham et al., 2008b). Their results showed that participants fixated the eyes and head region preferentially over other scene regions, but still made fixations to body parts and objects as well. The initial fixations to an image were directed most often to the eyes and heads equally across tasks, however at later time points, a higher fixation proportion for the eye region was observed when describing where the people in the images were directing their social attention compared to simply describing the objects in the image. These findings imply that the eyes are especially important for social descriptions of a scene. Results also showed that the eye and head regions were fixated more only when both the number and activity of people in a scene increased, and not when either activity level or person number was increased independently. These findings demonstrate that viewing the eye and head regions is essential for the extraction of social attention information and further highlights the role of these areas for understanding the social aspects of the actions and interactions of others (Birmingham et al., 2008b).

Emotion is also an integral social element of scenes that can affect eye movement. For example, when emotional and non-emotional scenes depicting people are presented in pairs, the emotional pictures are more likely to be fixated than the neutral pictures. Moreover, emotional pictures are fixated longer, especially initially, compared to neutral scenes (Calvo and Lang, 2004). This bias in viewing time is likely due to increases in attention when affective signals are detected in a scene as compared to when only non-emotional cues are present. Ramping up attention networks serves to promote further investigation and processing of affective scenes relative to non-emotional scenes and is an adaptive response related to the potential of emotional images to contain information important for our survival (Nummenmaa et al., 2006). Of high emotional significance within these images are faces since they can convey information alerting us to biological and social changes in the environment (Palermo and Rhodes, 2007), a process that occurs 100-300 ms after stimulus onset (Eimer and Holmes, 2007). Because of their importance, healthy humans have been shown to rapidly and automatically orient towards faces



in a scene (Sasson et al., 2007), with initial fixations most commonly directed to either the eyes or the mouth (Eisenbarth and Alpers, 2011). However, which area is most important seems to depend on the type of expression. A study by Eisenbarth and Alpers (2011) showed that the eye region is attended to more for sad and angry expressions, the mouth is fixated longest when viewing happy expressions, while both the eyes and the mouth are equally fixated for fearful and neutral faces. These results suggest that each emotion is viewed and decoded based on the region most characteristic for that emotion (Eisenbarth and Alpers, 2011).

In the real world, a scene is likely to contain a combination of social and emotional cues that must be pieced together in order to comprehend the situation as a whole. By studying eye movements related to viewing complex images, we can better understand the influences looking behavior has on how we extract, process, and apply this information during social interactions.

#### **1.3.4 Eye Movements and the Brain**

Research shows that the control and direction of saccadic eye movements and subsequent fixations interacts closely with the brain circuitry involved in attention and the evaluation of our actions (Corbetta et al., 1998; Najemnik and Geisler, 2005; Sohn and Lee, 2006; Schütz et al., 2011). Single unit studies of monkeys performing visually guided saccadic eye movements have recorded oculomotor activity in many cortical and subcortical regions including the frontal eye fields (e.g. Bizzi, 1968; Bruce and Goldberg, 1985), supplementary eye field (e.g. Schlag and Schlag-Rey, 1987), dorsolateral prefrontal cortex (e.g. Funahashi et al., 1991), posterior parietal cortex (e.g. Mountcastle et al., 1975; Robinson et al., 1978; Andersen, 1989), caudate (e.g. Hikosaka et al., 1989), and thalamus (e.g. Petersen et al., 1985). Responses in these areas to visual stimuli are also modulated by their behavioral relevance, in that stimuli presented at task-relevant locations generate different responses than stimuli located at task-irrelevant positions (e.g. Goldberg and Wurtz, 1972; Bushnell et al., 1981; Steinmetz et al., 1994; Robinson et al., 1995; Colby et al., 1996).

Human neuroimaging and transcranial magnetic stimulation studies of attention and visual saccade tasks have shown activation in similar regions of frontal and parietal cortex, further supporting the role of these anatomical areas in both attention and eye movement processes (see Corbetta, 1998; Corbetta et al., 1998). For example, the frontal eye fields has been

found to play a role in visual selection processes (Grosbras and Paus, 2002; Muggleton et al., 2003) as well as saccadic initiation (e.g. Bruce and Goldberg, 1985; Pierrot-Deseilligny et al., 1991; Rivaud et al., 1994) and reaction time (Connolly et al., 2005), while the parietal cortex is important for making voluntary saccades (see McDowell et al., 2008). Connections between the frontal eye fields and parietal cortex likely support the execution of visual fixations (Rivaud et al., 1994). Increases in supplementary eye field activation in humans has been linked to tasks requiring more cognitively complex saccades, particularly those associated with remembering and generating motor sequences (McDowell et al., 2008). Another frontal area, the dorsolateral prefrontal cortex, is involved in saccade inhibition, memory-guided saccades, and making intentional or anticipatory saccades especially in decision-making processes (Pierrot-Deseilligny et al., 2004). Interestingly, the cerebellum has also been implicated in saccade tasks, with the relative volume of the vermis being correlated with saccade accuracy (Ettinger et al., 2002). Together, these and other studies support the involvement of an expansive network of cortical regions including the frontal eye fields, supplementary eye fields, dorsolateral prefrontal cortex, and regions of posterior parietal cortex that are responsible for generating and controlling fixational and saccadic eye movements (Pierrot-Deseilligny et al., 2004; Medendorp et al., 2005).

## **1.4 Social Cognition Disorders**

Social cognition has been defined as the ability to use the beliefs and intentions of others in order to interpret and predict their behavior, as well as being able to apply this knowledge during complex social situations and relationships (Brothers, 1990; Baron-Cohen et al., 2000). Proper viewing, extraction, and processing of social cues and information as discussed in Sections 1.2 and 1.3.3 is critical for successful social interactions. For most of us, identifying and deciphering salient social signals is a rapid and automatic process. However, individuals with social cognition disorders have difficulties gathering and interpreting socially relevant information, though the exact source of such impairments are not clear. Two disorders in particular that are characterized by deficits in social functioning are autism spectrum disorder and schizophrenia (American Psychiatric Association, 2000). Investigations into the impairments and underlying causes of these disorders suggest abnormal visual search patterns, as well as differences in brain activity, as contributing factors. The following sections briefly discuss each disorder and present the results of research aimed at elucidating the underpinnings of their social impairments.

### **1.4.1 Autism Spectrum Disorder**

Autism spectrum disorder (ASD) represents a range of neurodevelopment disorders including autism, the most severe form, and a milder form known as Asperger syndrome, most of which are characterized by social impairments, repetitive and stereotyped behaviors, and difficulties in communication. The National Institute of Neurological Disorders and Stroke (2009, [http://www.ninds.nih.gov/disorders/autism/detail\\_autism.htm](http://www.ninds.nih.gov/disorders/autism/detail_autism.htm)) estimates that six children out of every 1,000 will be diagnosed with some form of ASD, with males being four times more likely to have ASD than females. Though variable, the most common social abnormalities present in individuals with ASD are withdrawal, diminished eye contact, a tendency to treat other people like inanimate objects, and a lack of attention to and understanding of the feelings of others (Baron-Cohen and Bolton, 1993).

Much research has gone into examining the exact nature of these social deficits. A relatively consistent finding is that individuals with autism show abnormalities in face perception

tasks, including memory for faces (Klin et al., 1999; Marcus and Nelson, 2001). Neuroimaging studies have demonstrated that activity in the fusiform gyrus is reduced during neutral face perception tasks, while activity in object sensitive areas of the lateral temporal cortex is increased (Schultz et al., 2000; Pierce et al., 2001). Individuals with autism also display impairments in the detection and perception of emotion in faces, which is likely related to observed decreases in amygdala activity when presented with emotional faces (Critchley et al., 2000; Howard et al., 2000; Adolphs et al., 2001). However, it is important to note that fMRI activation is highly sensitive to eye movement patterns made during face processing tasks, and thus presents a confounding factor when analyzing or interpreting fMRI data that was collected without controlling for eye movements (Morris et al., 2007). It will be important for future studies to monitor both brain activity and eye movement of participants to eliminate any potential misinterpretation of fMRI activity to socially relevant stimuli.

Interestingly, a common finding in persons with ASD is that they have abnormal viewing patterns when looking at social stimuli (Klin et al., 2002; Pelphrey et al., 2002). For instance, two-year-old children with autism view the eyes of faces less than healthy children, but view the mouth area more. This study also showed that the children's eye fixation patterns correlated with their social functioning, with fewer fixations of the eyes predicting increased social disability (Jones et al., 2008). These viewing abnormalities can be exhibited by other members of the family, as younger siblings of children diagnosed with autism also show a decreased tendency to view the eye region (Merin et al., 2007) as do the parents of autistic children (Adolphs et al., 2008). Further research has proposed that for ASD individuals, fixating the eyes is linked with negatively valenced over arousal in limbic regions such as the amygdala (Dalton et al., 2005), which may fuel their aversion to fixating the eye region of faces (Richer and Coss, 1976; Spezio et al., 2007).

However, the social impairments in autism may be the result of neural processing abnormalities to social stimuli rather than the result of improper viewing of these stimuli. Individuals with autism display differences in STS activation compared to healthy controls, a region known to be highly involved in the processing of social information. One study found that while both neurologically normal and autistic participants showed activity in the STS in response to detecting the eye gaze changes of an animated character, only neurologically normal participants showed differential activity for congruent and incongruent gaze shifts (Pelphrey et

al., 2005). This difference was not related to differences in the degree to which individuals with autism attended to the stimuli, as their behavioral accuracy ratings for detecting the eye gaze changes did not differ from that of the neurologically normal comparison participants. Therefore, the lack of differential STS activity in autistic individuals is thought to be related to an inability to link the perceptual representation of eyes moving and the simultaneous representation regarding a character's goals and motives to determine the intentions of another person (Pelphrey et al., 2005). Such findings suggest that for individuals with autism, their aversion to and difficulties with social information may not be limited to eyes and faces, but could extend to any stimulus with high social content (Dalton et al., 2005). Indeed, a study by Riby and Hancock (2008) found that individuals with autism spent less time than control participants viewing both faces and people in pictures of social interactions (Figure 1-7). This notion is further supported by reports indicating impaired judgment of mental states in people with autism (Courchesne, 1997).

Clearly more research is needed to fully understand the reasons behind the debilitating social difficulties experienced by individuals with autism. However, it is becoming apparent that the abnormal focus on local rather than global features plays an important role, perhaps due to underlying abnormalities in deploying attention to the appropriate features for gathering social information (Dakin and Frith, 2005; Neumann et al., 2006). Whether the activation differences in regions like the fusiform, amygdala, and STS stem from or are the result of improper viewing of social stimuli has yet to be determined.

#### **1.4.2 Schizophrenia**

Similar to ASD, schizophrenia is characterized by a deficit in social functioning resulting in social isolation. This debilitating disorder affects around one percent of the population in all cultures, with women and men being affected equally (American Psychiatric Association, 2000). Unlike ASD whose symptoms can be identified early in life, individuals with schizophrenia do not present with the disease until their 20s or 30s. The most significant risk factor for schizophrenia is family history; other potential risk factors have been investigated, such as birthplace and season, socioeconomic status, and maternal infections, but conclusive evidence in support of these ideas is still lacking (Bromet and Fennig, 1999; Mortensen et al., 1999; Lewis

and Lieberman, 2000). There are at least five types of schizophrenia, each expressing different combinations of positive symptoms, such as hallucinations and delusions, and negative symptoms, such as flattened affect and avolition (American Psychiatric Association, 2000). However, the ‘founding fathers’ of schizophrenia recognized that these symptoms were not specific to schizophrenia, and thus emphasized that this disorder is a brain disease defined by abnormalities in cognitive processes that hinder one’s ability to think in logical ways (Bleuler, 1911; Kraepelin et al., 1919).

Indeed, studies report that individuals with schizophrenia display deficits on tests of higher cognitive functions, especially those utilizing controlled and active information processing like verbal and visuo-spatial working memory and language skills (see Antonova et al., 2004). It has further been suggested that schizophrenia is associated with a failure to monitor the mental states of one’s self and others, leading to problems predicting and understanding another’s behavior, particularly in social situations (Frith, 1992). Research supports this idea, showing individuals with schizophrenia have difficulties extracting and integrating information from social contexts, and tend to misidentify the rules or affect of a situation, which affects their ability to make correct emotional and mental state inferences (Edwards et al., 2002; Harrington et al., 2005; Monkul et al., 2007; Green et al., 2008).

Neuroimaging studies of individuals with schizophrenia report structural differences throughout the brain. Compared to healthy controls, patients have smaller total brain, gray matter, and white matter volumes. More specifically, regions of the inferior frontal cortex, lingual gyrus, and superior temporal cortex are affected, particularly in the left hemisphere, and the structural alterations observed in these regions have been linked to various cognitive deficits (Antonova et al., 2005). Reductions in amygdala and FFA activation have been observed in people with schizophrenia during basic social cognition tasks, such as viewing faces and recognizing emotion (Hempel et al., 2003; Quintana et al., 2003), as well as for more complex social tasks like judging trustworthiness (Pinkham et al., 2008). However, these activation differences may occur in only some subtypes of schizophrenia (Williams et al., 2004; Pinkham et al., 2008). Individuals with schizophrenia additionally demonstrate decreases in prefrontal cortices when performing social judgments and mental state attribution tasks (Russell et al., 2000; Brunet et al., 2003; Pinkham et al., 2008), as well as decreased engagement of the STS during theory of mind tasks (Sugranyes et al., 2011).

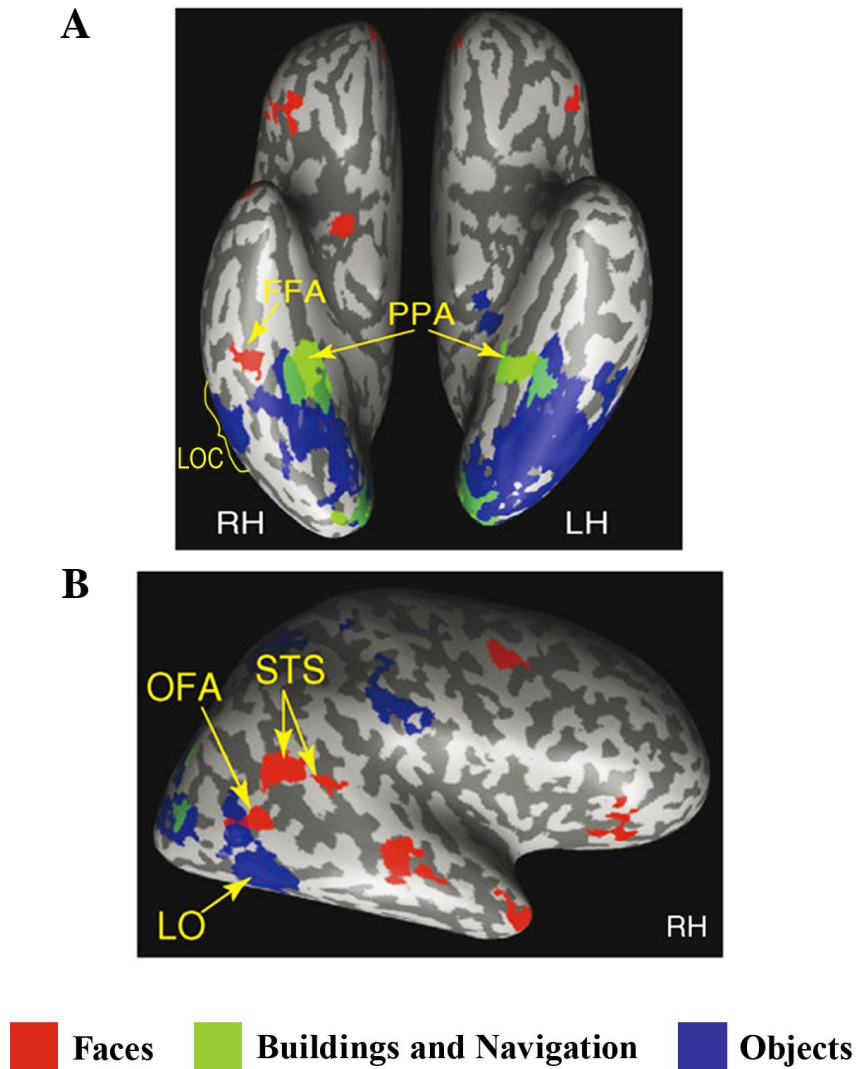
The altered brain activity during social tasks in schizophrenia might be related to abnormal looking behavior. Compared to healthy controls, people with schizophrenia generally make fewer fixations, but have longer fixation and saccade durations (Bestelmeyer et al., 2006). They also perceive objects and scenes in a fragmented manner, directing their focus to irrelevant details, especially when viewing complex scenes and faces (Frith et al., 1983; Gordon et al., 1992; Kurachi et al., 1994; Phillips and David, 1997; Streit et al., 1997). These findings indicate that schizophrenia is associated with impairments in forming perceptual gestalts (Frith et al., 1983; John and Hemsley, 1992). Similar to individuals with autism, individuals with schizophrenia avoid viewing the most salient features of emotional face stimuli and show impairments related to the identification of emotional expressions (Green et al., 2003). These visual scanning abnormalities along with the structural and functional brain deficiencies leave schizophrenia patients unable to properly integrate and apply social information and often prevent them from creating and maintaining social relationships.

## 1.5 Conclusions

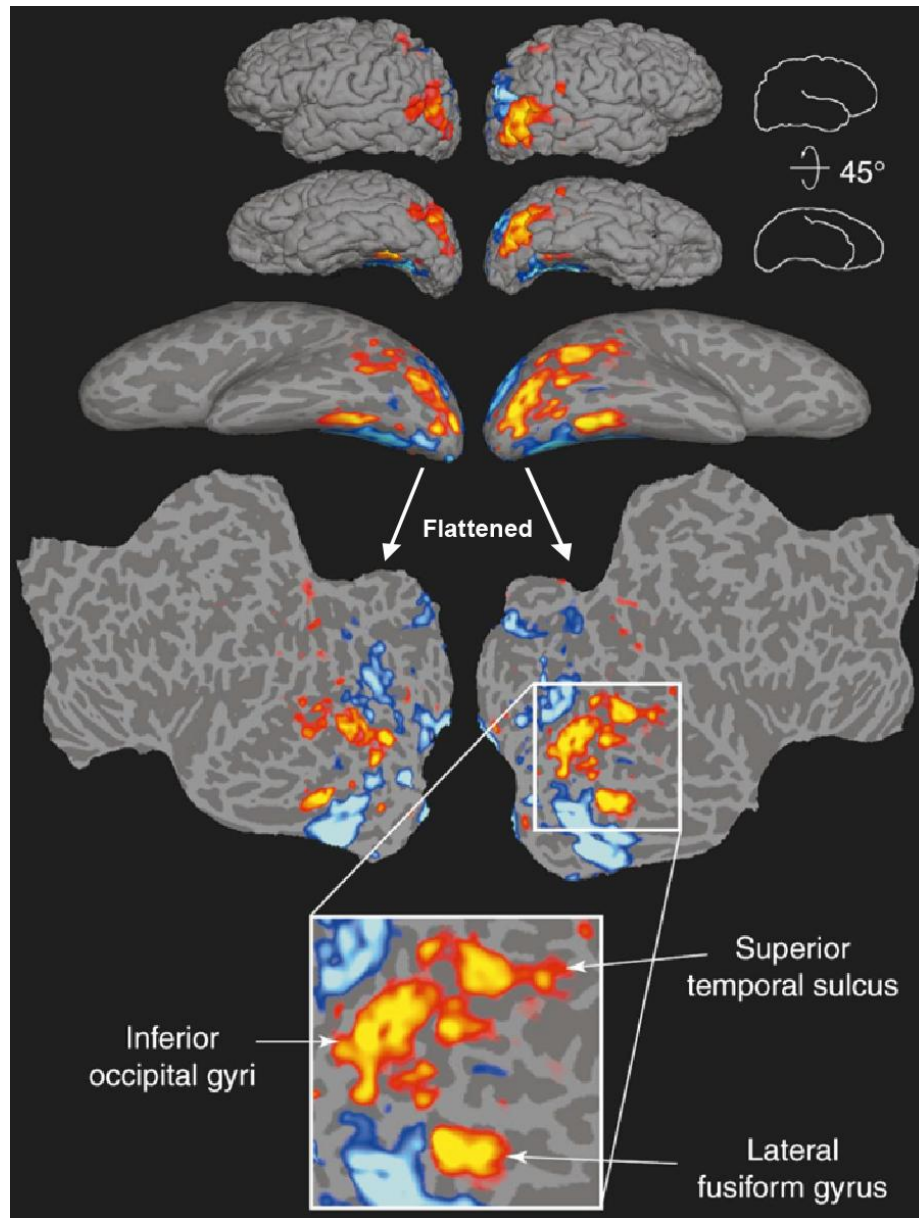
This section outlined how humans view and process visual information from our surroundings including information about objects, people, and scenes. Of particular importance is our ability to appropriately identify, extract, and interpret salient social cues from the environment and use them to predict the behavior of others, as well as guide our own behavior. However, there are still gaps in our knowledge regarding how more realistic scenes are viewed and processed by the human brain. Particularly in regards to the social versus non-social scene elements, and whether there are differences in how these aspects of a scene are viewed and interpreted when presented simultaneously in a single image, much like how they would be experienced in the real world. The isolation experienced by individuals with social cognition disorders may stem from abnormalities in the circuitry linking how the social features of an image are viewed with relevant brain regions. Investigating the eye movement and brain activation patterns of healthy individuals to social and non-social interpretations of identical complex scenes may aid in understanding the underlying basis for the deficiencies present in social cognition disorders. The information presented here provides a basis for understanding the rationale and objectives behind the experiments outlined in Chapters 3 and 4.



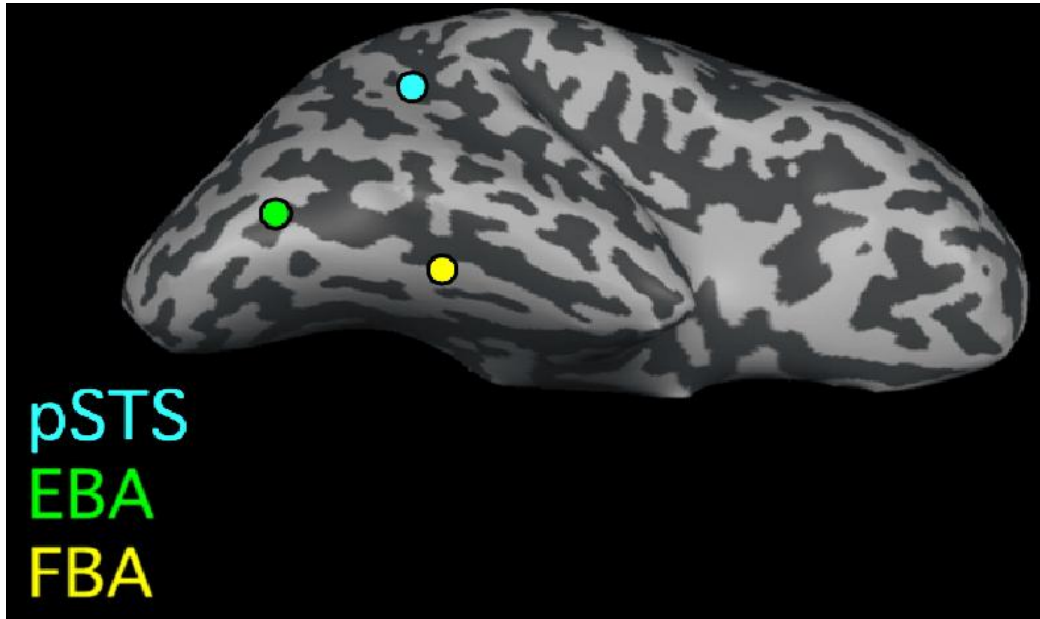
## 1.6 Figures



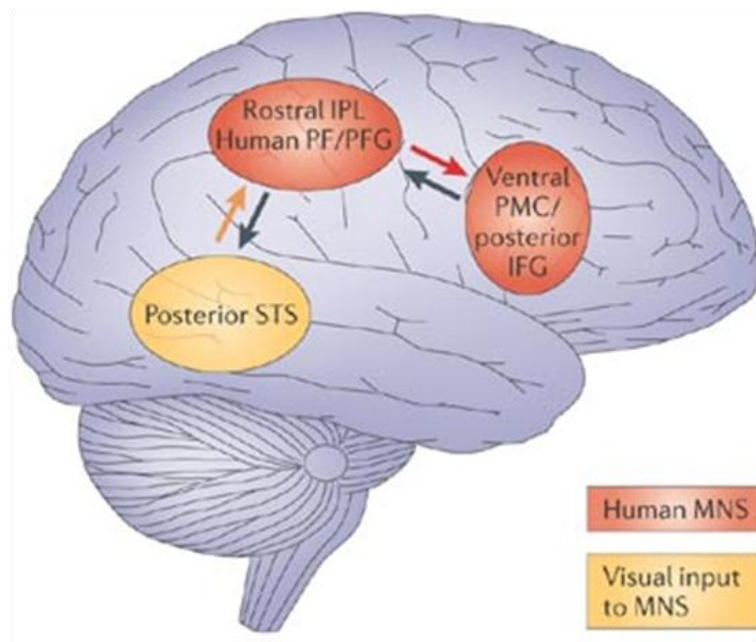
**Figure 1-1.** Differential activation for each stimulus category mapped onto an inflated brain: **A.** a ventral view and **B.** a lateral view of the right hemisphere (RH). Face-selective activation is displayed in red, object-selective activation is depicted in blue, and activation selective for buildings and navigation is displayed in green. Abbreviations: FFA, fusiform face area; LH, left hemisphere; LO, lateral occipital; LOC, lateral occipital complex; OFA, occipital face area; PPA, parahippocampal place area; STS, superior temporal sulcus. Figure and caption adapted from another source (Cohen Kadosh and Johnson, 2007).



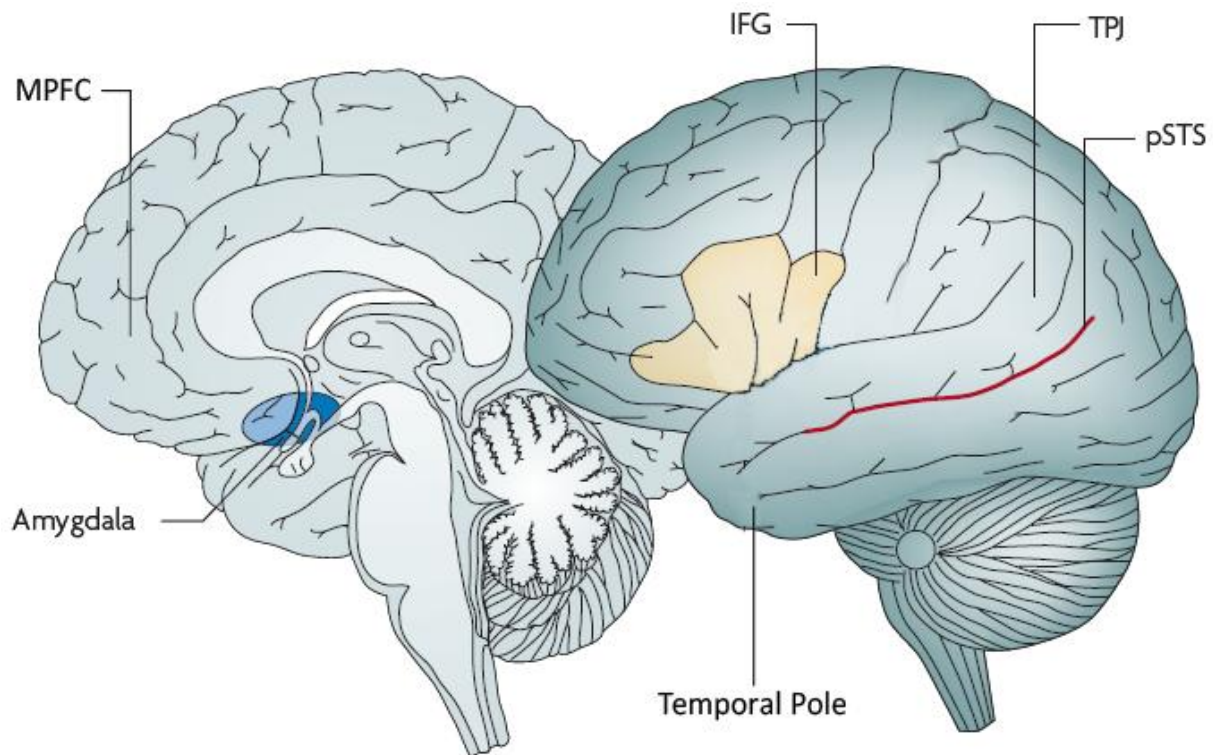
**Figure 1-2.** Locations of the regions that comprise the core system for visual analysis of faces, illustrated by functional magnetic resonance imaging results from a single subject (Haxby et al., 1999). Regions shown in red to yellow responded more to faces than to houses. Regions shown in blue responded more to houses than to faces. The upper figures are lateral views of the folded cortical surface. The next row of images shows the cortical surfaces of each hemisphere tilted back  $45^\circ$  to show both the lateral and ventral surfaces of the temporal lobe. In the next images, the cortical surfaces are inflated to show the cortex in the sulci, indicated by a darker shade of gray. The lower images show the entire cortical surface of each hemisphere flattened into a two-dimensional sheet. Figure and caption adapted from another source (Haxby et al., 2000a).



**Figure 1-3.** Schematic illustration of key brain areas involved in the perception of human bodies, body parts, and bodily movements. The extrastriate body area (EBA, green) is located in the inferior temporal sulcus, and the fusiform body area (FBA, yellow) is located in the lateral fusiform gyrus. Both regions respond strongly and selectively to static and dynamic images of human bodies and body parts. A region in the posterior superior temporal sulcus (pSTS, light blue) responds preferentially to human biological motion. Figure and caption adapted from another source (Kontaris et al., 2009).



**Figure 1-4.** Schematic overview of the frontoparietal mirror neuron system (MNS; red) and its main visual input (yellow) in the human brain. An anterior area with mirror neuron properties is located in the inferior frontal cortex, encompassing the posterior inferior frontal gyrus (IFG) and adjacent ventral premotor cortex (PMC). A posterior area with mirror neuron properties is located in the rostral part of the inferior parietal lobule (IPL), and can be considered the human homologue of area PF/PFG in the macaque. The main visual input to the MNS originates from the posterior superior temporal sulcus (STS). Together, these three areas form a 'core circuit' for imitation. The visual input from the STS to the MNS is represented by an orange arrow. The red arrow represents the information flow from the parietal MNS, associated with the motor properties of the action, to the frontal MNS, which is more concerned with the goal of the action. The black arrows represent efference copies of motor imitative commands that are sent back to the STS to allow matching between the sensory predictions of imitative motor plans and the visual description of the observed action. Figure and caption adapted from another source (Iacoboni and Dapretto, 2006).

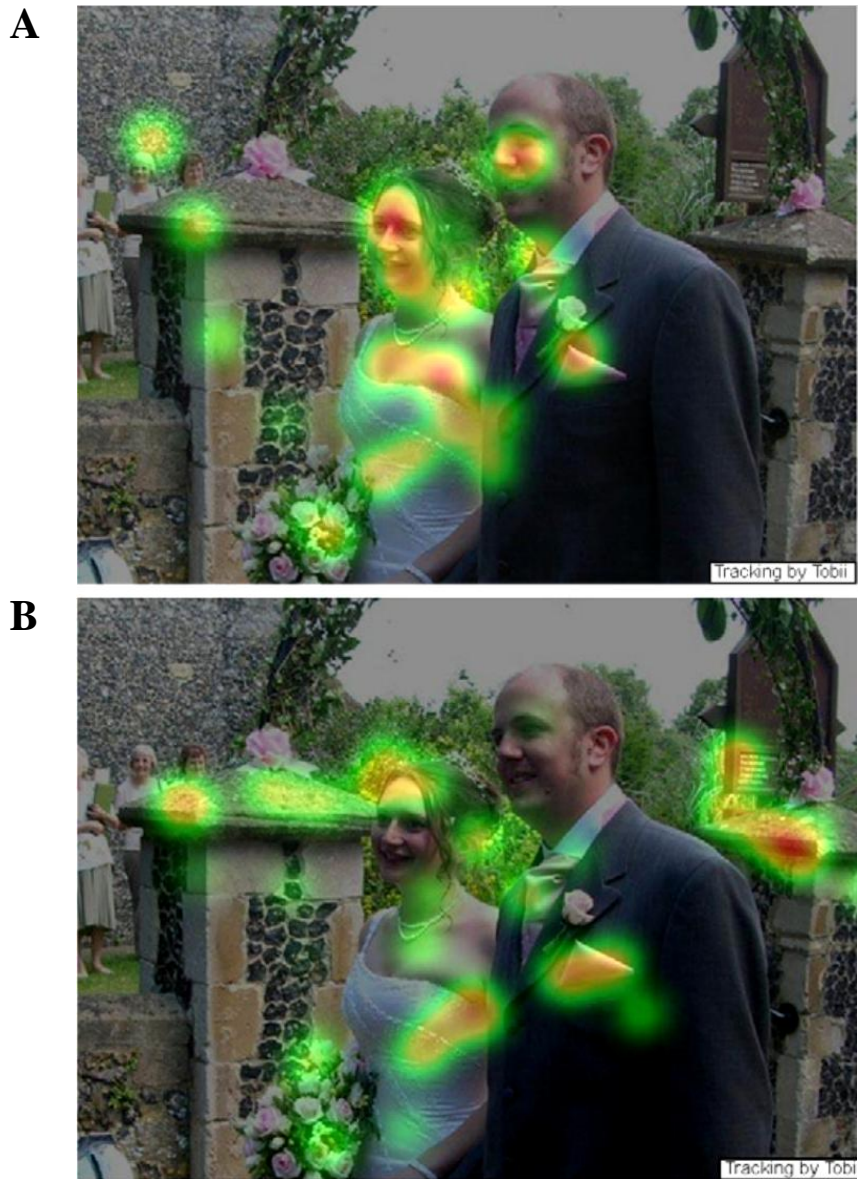


**Figure 1-5.** Regions of the social brain. Regions that are involved in social cognition include the medial prefrontal cortex (MPFC) and the temporo-parietal junction (TPJ), which are involved in thinking about mental states, and the posterior superior temporal sulcus (pSTS), which is activated by observing faces and biological motion. Other regions of the social brain on the lateral surface are the inferior frontal gyrus (IFG) and temporal pole. The amygdala, located on the medial surface, is also involved in social cognition. Figure and caption adapted from another source (Blakemore, 2008).



**A****B****C****D**

**Figure 1-6.** Recordings made by Alfred Yarbus (Yarbus, 1967) of a participant's eye movements when viewing a picture with different questions in mind. **A.** The picture - 'They did not expect him' by I.P. Repin. **B.** Pattern of saccades and fixations when instructed to 'remember the clothes worn by the people'. **C.** Pattern when instructed to 'remember the positions of the people and objects in the room'. **D.** Pattern when instructed to 'estimate how long the 'unexpected visitor' had been away.' Figure and caption adapted from another source (Land, 2006).



**Figure 1-7.** Representative fixation patterns for **A.** healthy controls, and **B.** individuals with autism on a social scene. Hotspots represent the location and relative amount of time spent fixating throughout the scene, with red indicating longer fixation times than green. Individuals with autism fixate faces and bodies less than healthy controls. Figure and caption adapted from another source (Riby and Hancock, 2008).

## **CHAPTER 2: Objectives and Rationale**



The deficits in social functioning in individuals with social cognition disorders like autism and schizophrenia may stem from impairments in identifying and processing social and emotional information. Studies have shown that these individuals have significantly different neural responses to social and emotional stimuli relative to control subjects (Pierce et al., 2001; Quintana et al., 2003; Johnston et al., 2005), and their eye movement records show abnormalities in looking behavior and scan paths when viewing social stimuli (Gordon et al., 1992; Manor et al., 1999; Williams et al., 1999). Currently it is not known if and how looking behavior affects the neural processing of emotional and social information. Determining the influence social versus non-social interpretations may have on the looking behavior and neural responses to complex scenes in healthy subjects is essential for understanding how the healthy brain processes social information. The knowledge gained from the healthy brain may also aid in identifying new research avenues for studying the neural underpinnings of the social and emotional deficits present in schizophrenia and autism. The experiments in this dissertation were constructed to characterize the eye gaze patterns and neural mechanisms involved in the processing and interpretation of complex social scenes in healthy individuals using eye tracking and functional magnetic resonance imaging (fMRI). This chapter will introduce the objectives and present the rationale behind each experiment.

## **2.1 Objective 1 – Characterize the eye movements elicited to complex social scenes under different interpretation contexts**

Previous studies suggest that our perception of the social world relies on the integration of stored experiences with contextual information obtained from our current surroundings (Bar, 2004). A first step and integral to this integration process is the proper viewing and extraction of salient social signals from the environment. The importance of this ability is often overlooked, and is usually only investigated when abnormal, for instance in individuals with social cognition disorders such as autism. These studies have shown that higher social functioning in autism is correlated with increased fixation time on mouths, while increased fixation on objects predicts the opposite (Klin et al., 2002). However, little is known about the looking behavior of healthy individuals when viewing social images, or how this viewing strategy for social information might differ from that used to extract non-social signal types from within a complex scene.

Therefore, Objective 1 sought to investigate how viewing strategy is altered by different interpretations of complex images in healthy individuals. Specifically, participants will have their eye movements recorded using an infrared eye tracker while they are presented with grayscale images depicting people involved in complex social situations. During the experiment, word cues will appear prior to each image instructing participants to interpret the following image based on socially or non-socially relevant aspects of the scene. The main hypothesis was that participants would spend more time viewing the people in the images, especially their heads, during socially relevant interpretations of the images, whereas non-social interpretations would have more fixations directed toward objects. The number and duration of fixations, as well as pupil diameter will be compared for each interpretation, and the distribution of fixations across scene regions will be examined. Chapter 3 discusses the fixation patterns associated with social and non-social interpretations of complex scenes.

## **2.2 Objective 2 – Characterize the neural responses elicited to complex social scenes under different interpretation contexts**

Neuroimaging research using separate isolated presentations of objects and faces indicate that the processing of these stimuli is carried out by different regions of the brain. However, these types of tasks do not accurately reflect the real world, as many different types of signals can be present in a single scene. Currently it is not known whether the same regions activated by presentations of isolated stimuli are also active when viewing different aspects of a single complex scene. Of particular interest are the regions associated with processing social versus non-social information since individuals with schizophrenia and autism mainly exhibit brain activation abnormalities in response to social stimuli. By determining if separate brain activation patterns can be generated to different interpretations of the same complex scene in healthy individuals, then future studies may be able to apply such a method as a more realistic means for investigating the social deficits in schizophrenia and autism.

In Objective 2, participants will have their brain activity recorded using fMRI while they are presented with grayscale images depicting people involved in complex social situations. During the experiment, word cues will appear prior to each image instructing participants to interpret the following image based on the social or non-social features of the scene. The main

hypothesis for this study being that brain activity will increase in regions associated with social cognitive processes like theory of mind, especially the STS, during social interpretations of the scenes, while non-social interpretations will produce greater activity in object related areas such as LOC and the parahippocampus. To test this hypothesis, the fMRI BOLD responses to each interpretation condition will be compared. Chapter 4 discusses the brain activation patterns associated with social and non-social interpretations of complex scenes.

## **CHAPTER 3: Study 1 - Different Eye Gaze Patterns for Social versus Non-Social Interpretations of Complex Scenes**

This work was submitted for publication to *NeuroImage*. It has been modified from its original format.

### 3.1 Abstract

The ability to interact appropriately with other people relies on proper viewing of social stimuli, evidenced by the abnormalities in viewing faces and other social stimuli that accompany social functioning impairments present in disorders such as autism and schizophrenia. Here, we studied eye movement patterns to modified images from a validated psychological assessment test (Thematic Apperception Test) depicting affectively and cognitively challenging human situations. Participants viewed the same set of images under different interpretation conditions (social: People, non-social: Things) while their eye movements were recorded. Analysis of the data revealed that during the socially relevant interpretation condition, there was a significant increase in the number and duration of fixations directed to the people in the images (versus other scene regions) compared to the non-social interpretation condition. During non-social interpretations on the other hand, participants viewed non-social scene regions (e.g. books, furniture) more often and for longer compared to the social interpretation. These data demonstrate that despite being presented with the same series of complex visual images, distinct eye gaze patterns were observed for social versus non-social interpretations.

## 3.2 Introduction

In the natural environment, we assess continually changing visual scenes for relevant cues that will help us to understand the significance of what we see. This is especially true during social encounters where changes in another person's facial expressions and body language relative to the environmental background must be extracted in order to decipher their associated mental states – an ability known as mentalizing or having a theory of mind (Premack and Woodruff, 1978; Frith et al., 1991; Frith and Frith, 1999). It is well known that in social cognition disorders, such as schizophrenia and autism, individuals often display impairments in identifying emotional expressions as well as difficulties in interpreting, explaining, and predicting the behavior and intentions of other people (Courchesne, 1997; Habel et al., 2000; Penn et al., 2000; Edwards et al., 2001; Kohler et al., 2003; Pinkham et al., 2003). These individuals are also known to exhibit abnormal viewing patterns in that they may not examine a scene for salient content in the same way as healthy people (Phillips and David, 1997; Adolphs et al., 2001; Klin et al., 2002; Pelphrey et al., 2002; Dakin and Frith, 2005; Bestelmeyer et al., 2006; Neumann et al., 2006; Green et al., 2008). In order to understand the underlying mechanisms responsible for the impairments present in social cognition disorders, it is important to understand how healthy individuals view and process complex social information.

Previous research suggests that sensorimotor as well as cognitive and affective processes work in concert to allow quick detection and evaluation of poignant stimuli from among other competing stimuli (Nummenmaa et al., 2006). One process that is essential for effective scene perception and interpretation is gaze control, or the act of purposely directing the eyes to various selected positions within a scene in real time (Henderson, 2003). These eye movements are not simply reflexive actions directed by the structure of the scene itself, but are also influenced by 'top-down' instructions from executive regions of the brain that are tied to the goals and intentions of the observer (Yarbus, 1967; Land, 2006). Gaze control is an active, dynamic process enabling the timely and strategic collection of task-relevant information from a scene; ensuring that critical areas are fixated first and more often than less informative areas (Churchland et al., 1994; Ballard et al., 1997; Land, 1999). Studies on reading, scene perception, and mentalizing have shown that the duration of fixation can also be an important indicator of processing depth with longer fixation durations reflecting deeper and more comprehensive

processing (Rayner, 1998; Findlay and Gilchrist, 2003; Henderson, 2003; Irwin, 2004; Underwood et al., 2004; Henderson, 2007; Klein et al., 2009). These findings are in accordance with the idea that eye movements reflect, as well as guide cognition (Grant and Spivey, 2003; Thomas and Lleras, 2007), but little is known about the nature of this link and its effects on gaze control when viewing complex scenes.

The ability to control gaze and attention based on current needs is useful for real world tasks. For example, we would not be able to assess the threat level of a person walking down an alleyway if other scene components like sidewalk cracks or the shapes of the buildings were not ignored in lieu of focusing on the facial expression and body posture of the potential threat. However, if we were searching for a set of keys thought to be lost in that alleyway, our gaze would need to be directed towards the sidewalks or other scene areas that could provide clues to their location. Elucidating how these different goals affect the way we view a complex scene is especially important. While a few studies have investigated gaze patterns to social scenes (e.g. Birmingham et al., 2008a), the relationship between eye movement patterns and cognitive goals has not been addressed since early attempts by Yarbus (1967). By studying eye movements produced during both social and non-social interpretations of the *same* complex scenes, we can better understand how thoughts and goals influence our looking behavior when the environment remains constant. Additionally, because eye movements are the behavioral outcome of attentional shifts, recording them generates a visible map of attention engagement locations (Henderson, 2003) that identifies scene regions essential for any type of interpretation. Other advantages of studying eye movements are that the numbers of movement types are limited, readily accessible and observable, and provide an excellent means to index mentalizing without relying on language, thus bypassing the many problems associated with self-reports and questionnaires (Nisbett and Wilson, 1977; Schwartz et al., 1999).

The goal of the present study was to investigate how the eye gaze patterns of healthy individuals are altered when examining the *same* series of complex visual scenes with *different* interpretive goals. Participants had their eye movements recorded with an infrared eye tracker while they were presented with the same set of images, but instructed to visually focus on and contemplate either the social aspects of the scene, including the actions and intentions of the people in the images (People condition), or the non-social aspects of the scene, including the inanimate objects or things in the scene (Things condition). The main hypothesis was that the

social interpretations would require more attentional and cognitive resources, which would be reflected by an increase in the number and duration of fixations during this condition, particularly to the people in the images. Conversely, we expected that non-social interpretations would be associated with fixations being directed more towards objects in the images than to people.



### **3.3 Methods**

#### **3.3.1 Participants**

Sixteen healthy participants with no history of medical, neurological, or psychiatric disorder provided written consent to participate in a study approved by the Institutional Review Board of West Virginia University. All had either normal or corrected-to-normal vision. Eye movement was collected simultaneously with fMRI data (presented in Chapter 4). Due to the technical limitations of the eye tracker, including inconsistencies in detecting the corneal-reflex and in identifying the pupil because of insufficient contrast between the pupil and iris, only the data from nine participants were included in the final eye movement analysis (5 female, mean age of  $29.4 \pm 5.4$  yrs, 1 left-hander). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). To view the forms used to determine participant handedness, see Appendix Section A.1.

#### **3.3.2 Stimuli**

Stimuli consisted of a subset of grey-scale drawings selected from the Thematic Apperception Test (TAT) series (Murray, 1943). These behaviorally validated images (e.g. Figure 3-1A; to view all 12 images see Appendix Section A.2) have complex and compelling contexts designed to explore the human condition. The contexts of these images are ideal for promoting active visual investigations and engagement. Not all of the images in the TAT series contain people, so we selected a subset of 12 drawings depicting scenes of a person or persons (with clearly-seen full or 3/4 facial views) involved in a potentially challenging situation or social interaction set amongst a number of background objects.

The original grey-scale cardstock images were scanned at 600 dots per inch to create bitmap images. These were centered on a grey background using Photoshop 7.0 (Adobe Systems, Inc; mean luminance and contrast were adjusted and equated for all stimuli). A grid of 13 crosshairs (+) was overlaid onto each image to create the final stimulus image (see Figure 3-1A). Separate bitmap images were generated for the word cues (People, Things, Crosshairs) that consisted of one cue word typed in white and centered on a grey background matching those of

the other stimuli (Figure 3-1B). All 12 manipulated TAT images were then paired with each word cue to construct the interpretation conditions.

### **3.3.3 Activation Task Design and Delivery**

The eye movement task consisted of three conditions that were presented to participants during an fMRI scan session. Data from the Crosshairs condition was not included as part of the current analysis, but is presented and discussed in Appendix Section A.3. Task timing was as follows: a single trial began with one of the word cues presented centrally for 3 seconds (s). After a 3 s blank grey screen, one of the 12 manipulated TAT images was presented for 20 s, followed by a 6 s blank grey screen which ended the trial (Figure 3-1B). Overall, there were 12 trials for each of the three conditions (i.e. 36 total word cue / manipulated TAT image pairs). Trials were divided into three counterbalanced runs so that each manipulated TAT image was shown only once per run. The order in which word cue / manipulated TAT image pairs were presented across the three runs was randomized.

The eye movement task was projected onto a Plexiglas screen situated at the foot of the MRI scanner bed via a PC running Windows XP and Presentation software (Version 11.3, Neurobehavioral Systems, Albany, CA, USA). Participants were placed in a supine position in the scanner and viewed the task through a mirror mounted on the scanner headcoil, with images subtending a 10° by 13° visual angle (Figure 3-1A, dashed arrows).

Before commencing each run of the experiment, participants first viewed a grid of 13 crosshairs to calibrate the eye tracking system. As described earlier, each manipulated TAT image was overlaid with the same 13-crosshair grid used for calibration. The calibration procedure was immediately followed by the respective experimental run consisting of the 3 s word cues paired with one of the 12 manipulated TAT scenes.

Prior to the beginning of the experimental session, participants were informed that each scene would remain on the screen for 20 s, during which time they were to investigate the image visually according to the preceding word cue. For the social or ‘People’ condition, participants were instructed to visually explore the image and mentally construct events relating specifically to the people depicted in each scene. For the non-social or ‘Things’ condition, participants were

to focus on the non-human items in the scene (e.g., book, violin) as the basis for creating mental scenarios involving the inanimate object.

### **3.3.4 Data Acquisition**

Eye position, fixation duration, and pupil diameter were recorded with a MRI compatible infrared iViewX eye tracking system (SensoMotoric Instruments GmbH, Teltow, Germany). In this setup, a corneal-reflection system tracked the corneal reflex and pupil location relative to the static camera to determine the location of participants' gaze on the visual stimulus. Eye data were sampled at 60 Hertz with an effective accuracy of one visual degree. Since eye movement data was collected simultaneously with fMRI data (see Chapter 4), the camera was mounted on the head coil of the MRI scanner and positioned to record eye movements from the right eye of each participant. The eye tracking data acquisition proceeded in iViewX (Version 1.06.01, SensoMotoric Instruments GmbH, Teltow, Germany) and was synchronized to Presentation software (Version 11.3, Neurobehavioral Systems, Albany, CA, USA). Prior to each run, eye position was calibrated using the grid of 13 crosshairs described above.

### **3.3.5 Data Analysis**

Eye movement measurements were extracted using BeGaze software (Version 1.2.76, SensoMotoric Instruments GmbH, Teltow, Germany). The default fixation-detection parameter for a 60-Hertz sampling rate required the point of gaze to remain stable for a minimum duration of 80 ms in order to be counted as a fixation. For the eye tracking data associated with each interpretation condition, we measured the number of fixations, fixation duration, and pupil diameter (the most commonly reported variables in related cognitive neuroscience literature). In addition to identifying differences in fixation number and duration between conditions, we determined the distribution of fixations within scenes, as well as the relationship between condition and fixation distribution. Thus, prior to analyzing the fixation data, regions within each scene associated with the People and Things interpretation conditions were outlined using the BeGaze software (e.g. the people and inanimate objects; see outlines on Figure 3-1A). The number and duration of fixations occurring in these areas of interest (AOIs) were then grouped into one of two categories: *people* or *things*.

Fixation data for each condition and AOI category were analyzed in IBM SPSS Statistics (Release 19.0.0, SPSS Inc.) using the General Linear Model and within-subjects factors of Condition (People, Things) and AOI (*people, things*). Significance was determined by  $p < 0.05$  (Greenhouse-Geisser corrected). Relevant pairwise comparisons ( $p < 0.05$ , Bonferroni corrected for multiple comparisons) were performed. Pupil dilation data were analyzed using a paired-samples t-test to identify any differences in pupil diameter between the two conditions.

## 3.4 Results

### 3.4.1 Pupil Dilation as a Function of Interpretation Condition

Quantitative analyses of pupil dilation showed no significant differences in pupil diameter between the People and Things conditions as determined by a paired-samples t-test ( $t(8) = -0.438, p = 0.673$ ). This result was not unexpected given that participants viewed the same set of images in each condition, with all scenes having been adjusted and equated for overall luminance and contrast. Means (M) and standard errors (SE) for pupil diameter as a function of Condition are displayed graphically in Figure 3-2 and listed in Table 3-1.

### 3.4.2 Number of Fixations as a Function of Interpretation Condition

Initial qualitative visual inspection of participants' eye gaze paths indicated unique patterns of fixations for the two conditions (Figure 3-3). Using the General Linear Model on the total number of fixations made by participants and within-subjects factors of Condition (People, Things) and AOI (*people*, *things*), we found that there was no significant main effect of Condition ( $F[1,8] = 0.579, p = 0.468$ ; Figure 3-4A, colored bars), which indicated there was not a significant difference in the total number of fixations between the two conditions. However there was a significant main effect of AOI ( $F[1,8] = 5.39, p = 0.049$ ), with the total fixations made to *people* AOIs having more fixations than the *things* AOIs. Means and SEs for the number of fixations as a function of Condition and AOI are listed in Table 3-2.

We also found a significant interaction effect between Condition and AOI ( $F[1,8] = 40.22, p < 0.001$ ), demonstrating a difference in the distribution of fixations within the images for the two conditions. This interaction was explored with pairwise comparisons using a Bonferroni correction. Analyses investigating the distribution of fixation numbers in each condition indicated that during the People condition, participants made significantly more fixations in *people* AOIs relative to *things* ( $p = 0.002$ ) AOIs (Figure 3-4A, patterned rectangles in green bar). Likewise, during the Things condition, the number of fixations occurring in *things* AOIs was significantly higher than the number of fixations made to *people* AOIs ( $p = 0.018$ ; Figure 3-4A, patterned rectangles in purple bar).

When examining the number of fixations in each AOI category across conditions, the number of fixations landing in *people* AOIs was greatest for the People condition relative to the Things condition ( $p = 0.004$ ; Figure 3-4A, bottom patterned rectangle in both colored bars). Conversely, the number of fixations directed to *things* AOIs was highest during the Things condition compared to the People condition ( $p = 0.001$ ; Figure 3-4A, top patterned rectangle in both colored bars).

### 3.4.3 Total Time Spent Fixating as a Function of Interpretation Condition

Differences in the total time spent fixating the images was examined using the General Linear Model and within-subjects factors of Condition (People, Things) and AOI (*people*, *things*). Means and SEs for fixation duration as a function of Condition and AOI are listed in Table 3-2. There was no significant main effect of Condition ( $F[1,8] = 1.79$ ,  $p = 0.217$ ; Figure 3-4B, colored bars), and no significant main effect of AOI ( $F[1,8] = 3.55$ ,  $p = 0.096$ ). However, there was a significant Condition by AOI interaction effect for the duration of fixations ( $F[1,8] = 34.56$ ,  $p < 0.001$ ), indicating differences between conditions regarding the distribution of fixation durations. Pairwise comparisons identified that in the People condition, participants fixated *people* AOIs significantly longer than *things* AOIs ( $p = 0.003$ ; Figure 3-4B, patterned rectangles in green bar). For the Things condition, significantly longer fixations occurred in *things* AOIs relative to *people* AOIs ( $p = 0.03$ ; Figure 3-4B, patterned rectangles in purple bar).

Finally, the fixation duration data as measured from an AOI across Condition perspective show that fixations in *people* AOIs were longest during the People condition relative to the Things condition ( $p = 0.002$ ; Figure 3-4B, bottom patterned rectangle in both colored bars). Fixations within *things* AOIs were longest during the Things condition compared to People ( $p = 0.001$ ; Figure 3-4B, top patterned rectangle in both colored bars).

### 3.4.4 Fixations in Head and Body AOIs as a Function of Interpretation Condition

To investigate the differences in fixation distribution between the social and non-social conditions further, we compared the number of fixations directed towards both the head and body AOIs in relation to the total number of fixations per condition. During the People condition, 26.5% of fixations were directed to the head, while 37.2% of fixations occurred in

body AOIs. These percentages for fixating the head and body AOIs during the People condition were much higher than *people* AOI percentages for the Things condition, where only 14.7% of fixations were to the head and 26.9% were to the body. We also calculated the fixation durations within the head and body AOIs compared to the total time spent viewing the images in each condition. During the People condition, head AOIs were fixated 28% of the time and body AOIs 33%, while during the Things condition head AOIs were fixated 14.3% of the time and body AOIs 27%. Taken together these data suggest that fixating a person's head is especially important when making inferences about the thoughts and actions of other people.

### 3.5 Discussion

Infrared eye tracking data revealed that although there was no difference in fixation number or duration between the social and non-social domains at the level of the whole scene (i.e. *total* number and length of fixations per Condition), the distribution of fixation numbers and durations to identical scenes were affected by the type of interpretation used. Specifically, we found that during social interpretations, participants focused longer and more frequently on the protagonists of the scene at the expense of other objects. In contrast, when participants were performing non-social interpretations of the images, there was an increase in the number and duration of fixations directed toward scene regions containing background objects, such as furniture.

These different patterns exhibited by participants during social and non-social interpretations of scenes are consistent with the traditional notion that a given task influences eye movements during scene viewing (Buswell, 1935; Yarbush, 1967). However, our study goes beyond previous studies investigating differential eye movement patterns because rather than using separate groups of participants or stimuli for each interpretation, we sought to determine if and how different interpretations of the same series of scenes would affect participants' eye movement patterns to those scenes. While presenting isolated stimuli does have its advantages, our paradigm more accurately reflects how we view the real world. For instance, a natural background environment generally remains constant, but how we cognitively think about and in turn approach that environment may change. Our design parallels this aspect of our environment by presenting identical sets of images under different interpretation conditions.

An interesting finding was that the number of fixations directed towards people in the images, as well as the duration of fixations in these areas, was higher for the social interpretation condition compared to the non-social condition. Our data are in accordance with other studies showing that fixation time increases as the social content and / or need to extract social information from a scene increases (Smilek et al., 2006; Birmingham et al., 2008a; Klein et al., 2009). For example, a study by Birmingham and colleagues (2008a) presented participants with scenes that contained either one person or three people that were depicted as being inactive or active and tracked their eye movements to investigate if the addition of more people or the activity level would alter participants' looking behavior. They found that increasing the social



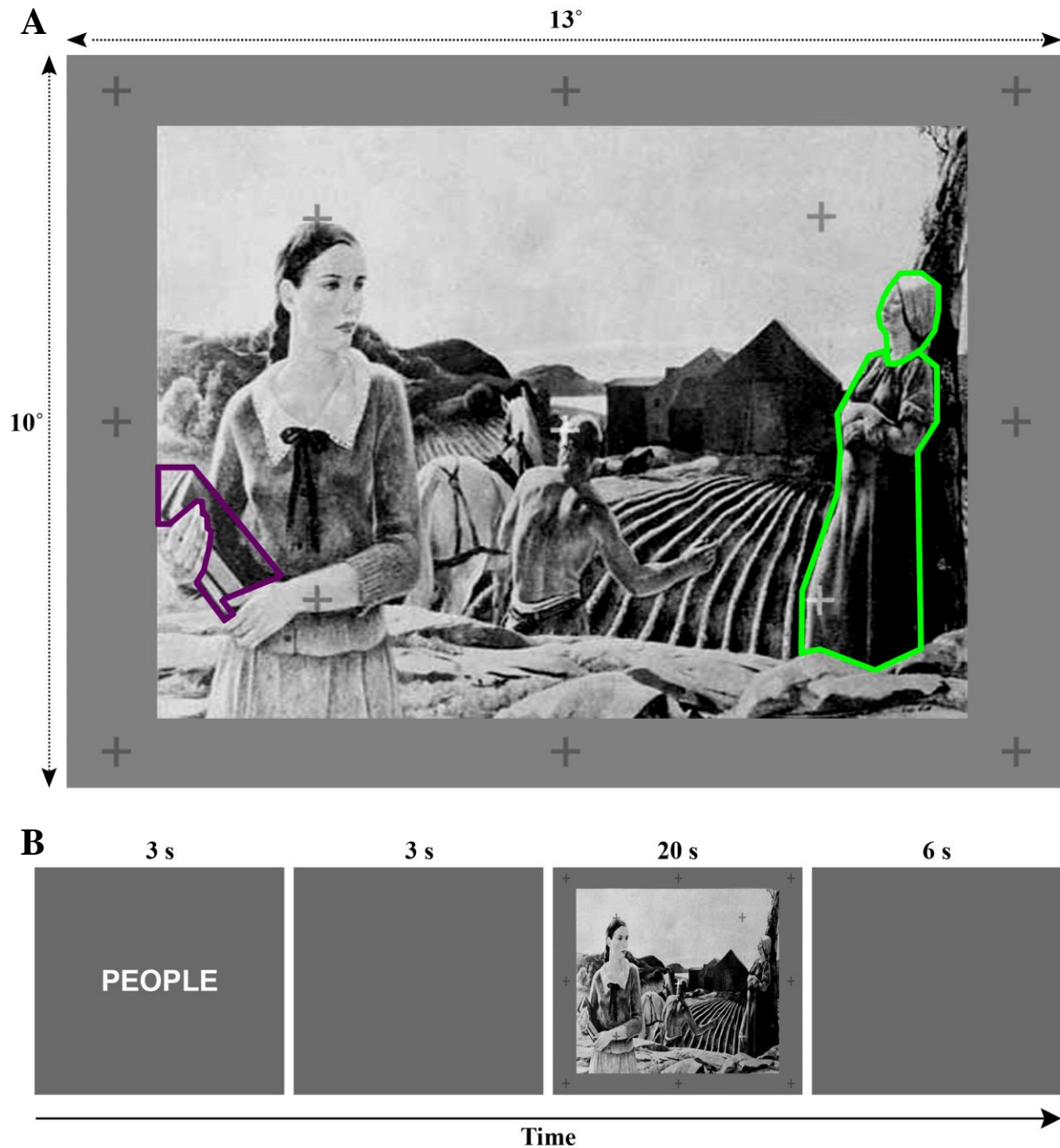
content of a scene (by increasing the number of people) only led to an increase in the number and duration of fixations to the eyes and heads when the people in the scene were actively engaged in an activity. The authors suggested that the social communication within a group of people in a scene draws viewers' attention towards the eye region in order to help extract information essential to understanding the social meaning behind their actions (Birmingham et al., 2008a). The data presented here support this suggestion, as we found significantly more fixations to *people* AOIs during the social interpretation condition and found that only the social interpretation was associated with a high percentage of fixations directed to the head region. These observations imply that information from the face is critical for interpreting the thoughts and intentions of others during a social interaction.

A study by Klein et al. (2009) also investigated the effects of social versus non-social content on looking behavior. They found that participants fixated longer on animations that, like our modified TAT pictures, were more socially and emotionally laden and evoked mental state attributions, compared to a control of randomly moving shapes. The authors suggested that the longer fixation durations were attributable to deeper processing related to incorporating mental state knowledge, which compared to other types of information, engages more prospective and retrospective processes that are complex and require higher resource demands. Here, without using different physical stimulus categories, we found increases not only in fixation durations but also in the number of fixations made to the people during social interpretations of scenes. Our observation of increased fixation durations specifically to *people* AOIs, especially the head region, supports the idea that these regions require deeper processing because they provide key information necessary for appropriately inferring the mental states of others.

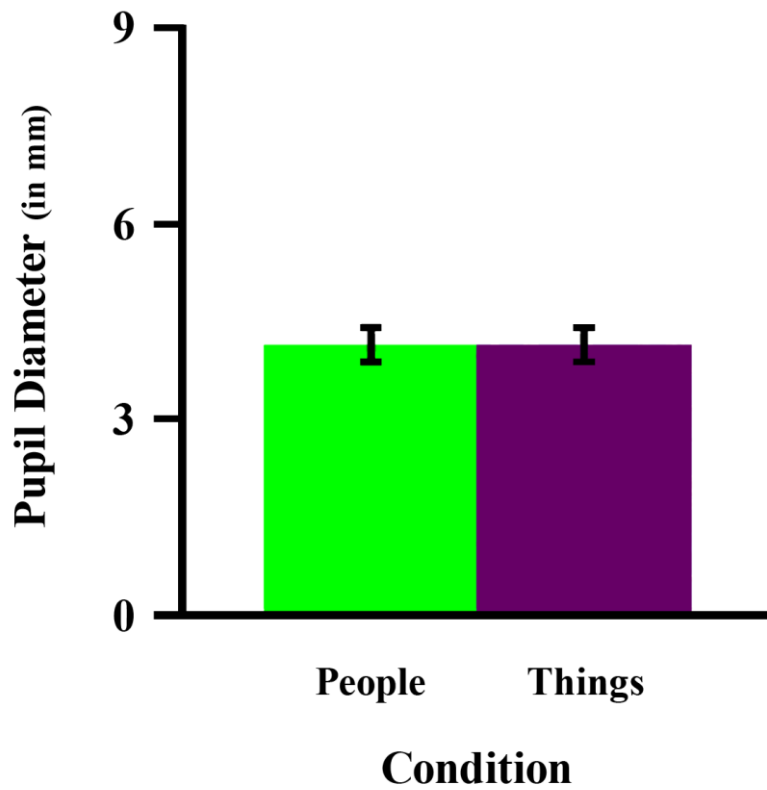
Studies on individuals with autism, who typically have difficulties in social situations, provide additional support for the importance of viewing the head and face regions during social encounters. Eye tracking research has shown that individuals with autism view people and faces within a scene less frequently than healthy participants do (Riby and Hancock, 2008). Individuals with schizophrenia also tend to view the social content of a scene abnormally, which may affect their ability to infer the mental and emotional states of other people (Green et al., 2008). Examining the link between eye movement patterns to social stimuli and the ability to processes and interpret the information extracted from those stimuli is critical to understanding the social impairments and deficits present in individuals with disorders like autism. The eye

tracking data reported here are important steps illustrating that healthy individuals have a natural inclination to visually isolate the aspects of a scene that are most relevant to their current goals. In particular, our data highlight the importance of viewing faces and bodies within a scene for the extraction of social information.

### 3.6 Figures and Tables



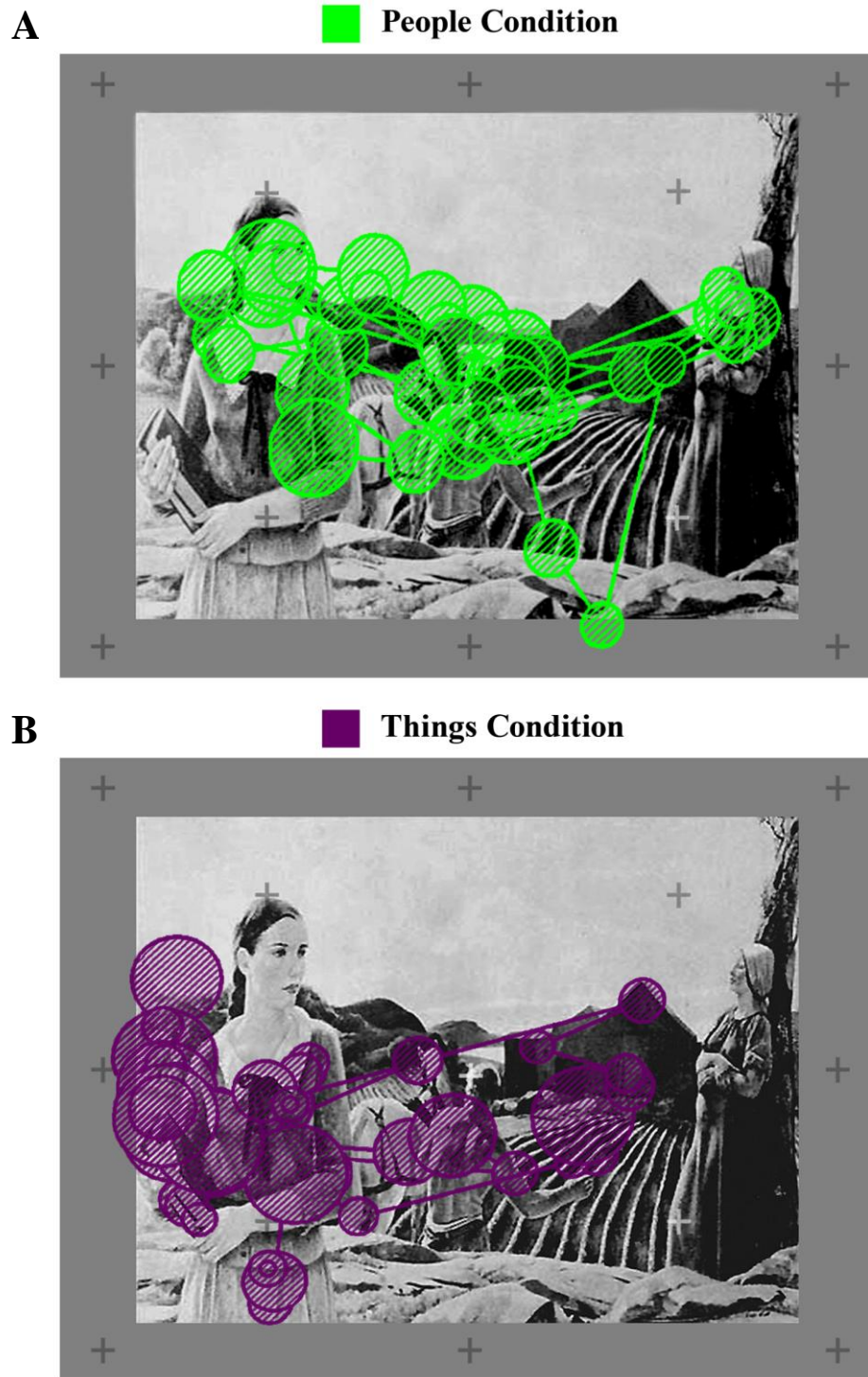
**Figure 3-1.** Stimuli and activation task. **A.** A representative manipulated TAT image from the 12 stimuli in our stimulus set. All TAT stimuli were overlaid with the same grid of 13 crosshairs and surrounded by a grey frame. Representative outlines for the two AOI categories are shown, with examples of a single *people* AOI in green, and a single *things* AOI in purple. AOIs were used for eye movement data analysis and were not visible to participants during the experiment. **B.** A single trial consisted of a 3 s word cue (e.g. People), followed by a blank grey screen for 3 s, and then the manipulated TAT image for 20 s. A 6 s blank grey screen separated trials. Other interpretation condition alternatives included Things and Crosshairs.



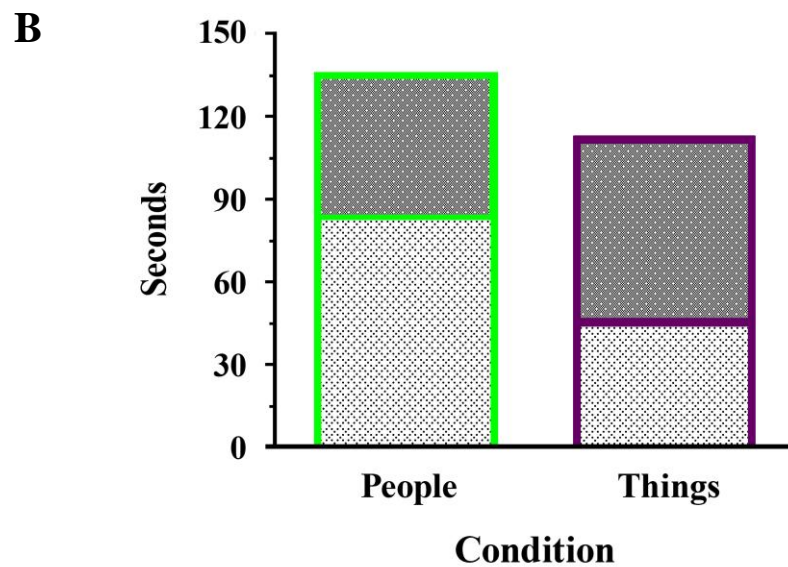
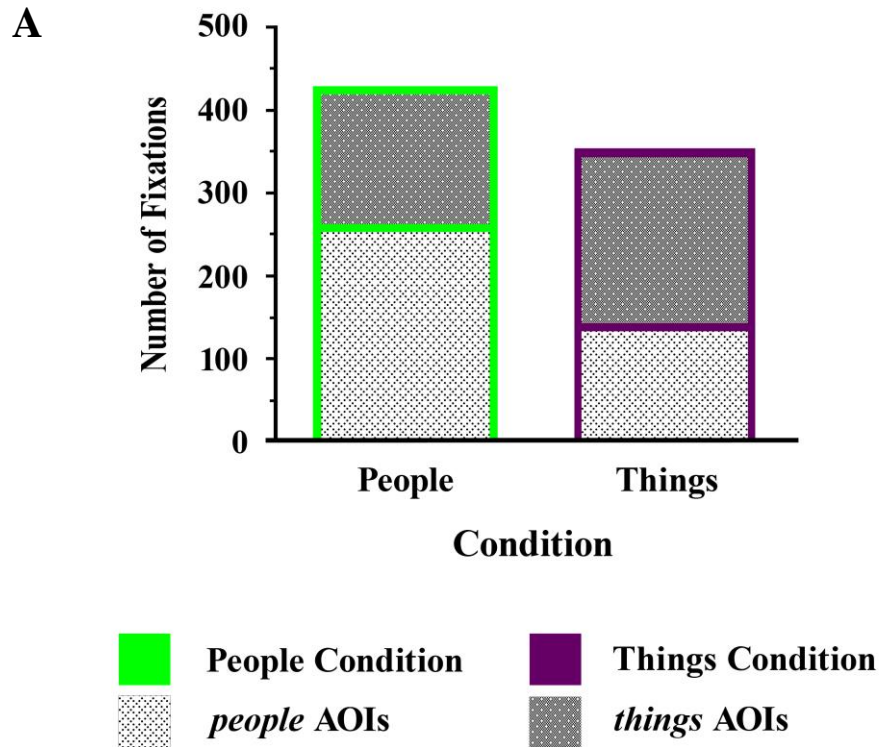
**Figure 3-2.** Graph displaying group data for overall mean pupil diameter in millimeters (mm;  $\pm$  standard error) during the People condition (green) and Things condition (purple).

**Table 3-1. Group means (M) and standard errors (SEs) for pupil diameter**

| <b>Condition</b> | <i>M</i> | <i>SE</i> |
|------------------|----------|-----------|
| People           | 4.147    | 0.262     |
| Things           | 4.168    | 0.258     |



**Figure 3-3.** Participants' eye gaze patterns were projected onto the manipulated TAT images to identify differences in how scenes were viewed for each condition. Displayed traces are representative single trial fixation patterns for the **A.** People condition, green, and the **B.** Things condition, purple. Areas fixated by the subject are designated by circles, which vary proportionally in size depending on fixation duration.



**Figure 3-4.** Graphs displaying group data for **A.** overall mean number of fixations for the two conditions (colored bars), and the distribution of those fixations across each of the AOI categories (patterned rectangles). Graphs displaying **B.** overall mean fixation duration for each condition in seconds (colored bars), and the distribution of those durations across the two AOI categories (patterned rectangles).

**Table 3-2. Group means (M) and standard errors (SEs) for eye fixation data**

| Condition | Number of Fixations |           | Fixation Duration |           | AOI           | Number of Fixations |           | Fixation Duration |           |
|-----------|---------------------|-----------|-------------------|-----------|---------------|---------------------|-----------|-------------------|-----------|
|           | <i>M</i>            | <i>SE</i> | <i>M</i>          | <i>SE</i> |               | <i>M</i>            | <i>SE</i> | <i>M</i>          | <i>SE</i> |
| People    | 395                 | 43.75     | 127464.56         | 13829.51  | <i>people</i> | 256.22              | 34.15     | 82324.89          | 11042.68  |
|           |                     |           |                   |           | <i>things</i> | 138.78              | 11.13     | 45139.67          | 3866.67   |
| Things    | 373.67              | 35.79     | 117880.67         | 9874.34   | <i>people</i> | 166.44              | 20.49     | 51796.33          | 6373.62   |
|           |                     |           |                   |           | <i>things</i> | 207.22              | 17.76     | 66084.33          | 4792.31   |



## **CHAPTER 4: Study 2 - Different Brain Activity Patterns for Social versus Non-Social Interpretations of Complex Scenes**

This work was submitted for publication to *NeuroImage*. It has been modified from its original format.

## 4.1 Abstract

Effective social interactions require the ability to properly identify and process the most salient social cues from within a complex scene. Previous research has focused on understanding the brain activity in response to isolated images of faces and objects; however, this method does not accurately reflect the real world, which usually contains a mixture of people, objects, and background context. The present study sought to investigate brain activation patterns to complex social scenes using modified images from a validated psychological assessment test (Thematic Apperception Test) depicting affectively and cognitively challenging human situations. Participants viewed the same set of images under different interpretation conditions (social: People, non-social: Things) while their brain activity was recorded. Functional magnetic resonance imaging (fMRI) revealed regions of right middle and superior temporal cortex that were selectively activated by the People condition compared to the Things condition, areas known for their role in social tasks. Brain activation in response to the Things condition was located in areas known to be associated with object processing, such as the parahippocampus. Taken together our data demonstrate that in healthy adults, brain activation patterns to identical scenes change markedly as a function of attentional focus and interpretation intention. Particularly striking, is that despite being presented with the same series of complex visual images comprised of multiple visual features, an explicit focus on the social aspects of the scenes preferentially activated the right middle and superior temporal cortices.

## 4.2 Introduction

A large body of neurophysiological and neuroimaging literature demonstrates that socially relevant stimuli, such as faces and bodies and the expressions they convey, produce distinctly different brain activation patterns from inanimate objects such as houses or complex scenes without social stimuli (Yin, 1969; Bruce et al., 1991; Turk and Pentland, 1991; Perrett et al., 1992; Sergent et al., 1992; Tanaka and Farah, 1993; Puce et al., 1995; Aguirre et al., 1996; Kanwisher et al., 1997; Sato et al., 1999; Nakamura et al., 2000; Downing et al., 2001; Hariri et al., 2002; Mitchell et al., 2002; Reed et al., 2003; Stekelenburg and de Gelder, 2004; de Gelder, 2006). Such specialized systems may develop when we learn the critical properties for identifying specific objects categories, enabling quick and efficient between-category discrimination (Mahon and Caramazza, 2003; Weisberg et al., 2007). The ability to differentiate between object categories is also important for evaluating a complex scene, where multiple objects in a scene can be represented simultaneously, providing a coherent view of the real-world environment 'at a glance' (Fei-Fei et al., 2007; Macevoy and Epstein, 2011). Relatively few studies have used these complex stimuli to evaluate visual perception (but see Spiers and Maguire, 2007; Hasson et al., 2010; Wolf et al., 2010), as most designs typically present faces, bodies, and background context in isolation and thus do not accurately reflect our natural environment.

Those studies that have investigated more complicated stimuli have made some important findings. For instance, a study by Kret and de Gelder (2010) discovered that bodily expressions were better recognized when they were congruent with the social context of the scene. However, interacting successfully with others goes beyond simply detecting a person in a scene. Social communication relies on the ability to decode the thoughts, beliefs, and intentions of other people, a process known as mentalizing or having a theory of mind (Premack and Woodruff, 1978; Frith et al., 1991; Frith and Frith, 1999). This ability has been investigated by having participants make inferences about the mental states of other individuals using a variety of approaches including stories (e.g. Fletcher et al., 1995; Saxe and Kanwisher, 2003), animated shapes (e.g. Castelli et al., 2000; Schultz et al., 2004), and occasionally more complex stimuli such as movies or interactive games (e.g. McCabe et al., 2001; Pelphrey et al., 2003; Grezes et al., 2004; Spiers and Maguire, 2006). Together these and other studies have shown that the

processes of mentalizing is associated with activity in a number of brain regions, with the posterior superior temporal sulcus (STS), temporo-parietal junction, medial prefrontal cortex (MPFC), and temporal poles being the most frequently reported (Frith and Frith, 2003; Gallagher and Frith, 2003).

Although examining brain activity to mentalizing is a task that is relevant to our daily lives, it still does not provide us with an accurate understanding of how we process our environment. For one, in the natural environment, the observer has many potential items to focus on not just the body position or thoughts of other people. Moreover, which items engage our attention and how the scene is interpreted as a whole will likely influence the observer's comprehension of the scene and their brain activation. Little is known about how our neural activity is affected when we evaluate a scene based on different components within that scene. Therefore, the goal of the present study was to investigate how brain activation patterns are altered when observers examine the *same* series of complex visual scenes with *different* interpretive goals.

To this end, we studied a group of healthy individuals with event-related fMRI. Participants were presented with the same set of images, but instructed to visually focus on and contemplate either the social aspects of the scene, including the actions and intentions of the people in the images (People condition), or the non-social aspects of the scene, including the inanimate objects or things in the scene (Things condition). The main question we sought to answer was how responses to visually scrutinizing socially relevant features in the visual scene and generating a *social* scenario might differ from the brain activity produced by a *non-social* interpretation. More specifically, we were interested in determining whether social interpretations relative to non-social interpretations would produce activation in cortical regions previously implicated in studies of mentalizing, including the MPFC and STS (Frith and Frith, 2006). Further, despite the people being present during both conditions would the social interpretation increase activity in face and body responsive regions. Lastly, we wanted to know if the activation pattern in response to the non-social condition would accurately reflect object processing by showing comparable activity to earlier studies presenting objects in isolation.

## **4.3 Methods**

### **4.3.1 Participants**

Sixteen healthy participants with no history of medical, neurological, or psychiatric disorder provided written consent to participate in a study approved by the Institutional Review Board of West Virginia University. All had either normal or corrected-to-normal vision. fMRI data collected from one participant had to be excluded due to excessive head movement artifacts, hence the data of 15 participants were included in the final analysis (8 female, mean age of  $26.9 \pm 5.4$  yrs, 2 left-handers). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). To view the forms used for participant screening and to determine handedness, see Appendix Section A.1.

### **4.3.2 Stimuli**

Stimuli consisted of a subset of grey-scale drawings selected from the Thematic Apperception Test (TAT) series (Murray, 1943). These behaviorally validated images (see Figure 3-1A for an example) have complex and compelling contexts designed to explore the human condition. The contexts of these images are ideal for promoting active visual investigations and engagement. Not all of the images in the TAT series contain people, so we selected a subset of 12 drawings depicting scenes of a person or persons (with clearly seen full or 3/4 facial views) involved in a potentially challenging situation or social interaction set amongst a number of background objects (to view all 12 images see Appendix Section A.2).

The original grey-scale cardstock images were scanned at 600 dots per inch to create bitmap images. These were centered on a grey background using Photoshop 7.0 (Adobe Systems, Inc; mean luminance and contrast were adjusted and equated for all stimuli). A grid of 13 crosshairs (+) was overlaid onto each image to create the final stimulus image. Separate bitmap images were generated for the word cues (People, Things, Crosshairs) that consisted of one cue word typed in white and centered on a grey background matching those of the other stimuli. All 12 manipulated TAT images were then paired with each word cue to construct the interpretation conditions.

### 4.3.3 Activation Task Design and Delivery

The activation task consisted of an event-related design spanning three experimental runs. Three conditions were presented during scanning, however the third condition was unrelated to the other two conditions and was not included as part of the present analysis. See Appendix Section A.4 for the results and a discussion of the third condition. Task timing was as follows: A single trial began with one of the word cues presented centrally for 3 s. After a 3 s blank grey screen, one of the 12 manipulated TAT images was presented for 20 s, followed by a 6 s blank grey screen which ended the trial (see Figure 3-1B). Overall, there were a total of 36 trials (the 36 word cue / manipulated TAT image pairs) with 12 trials per condition. Trials were divided into three counterbalanced runs so that each manipulated TAT image was shown only once per run, with the order in which word cue / manipulated TAT image pairs were presented across the three runs being randomized.

The activation task was projected onto a Plexiglas screen situated at the foot of the scanner bed via a PC running Windows XP and Presentation software (Version 11.3, Neurobehavioral Systems, Albany, CA, USA). Participants were placed in a supine position in the MRI scanner and viewed the activation task through a mirror mounted on the scanner headcoil, with images subtending a 10° by 13° visual angle (see Figure 3-1A, dashed arrows).

Before the scanning session began, participants were informed that each scene would remain on the screen for 20 s, during which time they were to visually investigate the image according to the preceding word cue. For the social or ‘People’ condition, participants were instructed to visually explore the image and mentally construct events relating specifically to the people depicted in each scene. For the non-social or ‘Things’ condition, participants were to focus on the non-human items in the scene (e.g., book, violin) as the basis for creating mental scenarios involving the (inanimate) object. In the third condition (Crosshairs), participants randomly focused on different crosshairs in the scene.

### 4.3.4 Data Acquisition

*Functional Images:* Whole brain axial volumes of BOLD activity were acquired using an eight-channel headcoil in a 3 Tesla GE Horizon LX MRI scanner (GE Medical Systems, Milwaukee, WI, USA). Functional images were acquired using a gradient echo spiral in-out

sequence. Twenty-two axial slices (4 mm thick, 1 mm gap) were obtained using the following parameters: TE / TR = 33.8 / 2000 ms; FOV = 240 mm (in-plane resolution = 1.875 mm); matrix = 128 X 128; bandwidth = 100. There were 199 volumes per imaging run, and three imaging runs in the experiment. Functional images were reconstructed offline with custom software (see below) and consisted of averaged spiral in-out trajectories, optimizing sampling from brain regions prone to susceptibility artifacts and MR signal drop out (Glover and Law, 2001).

*Anatomical Images:* We acquired a whole brain T1-weighted anatomical volume with identical slice prescription to functional images, as well as a whole brain high-resolution anatomical spoiled gradient-recalled volume (SPGR; voxel size = 1.2 mm x 0.9375 mm x 0.9375 mm; FOV = 240 mm; matrix = 256 X 256; 124 slices with 50% overlap) for subsequent overlay of activation data.

#### **4.3.5 Data Analysis**

Functional images were reconstructed offline using routines written in C (Gary Glover, Stanford University, CA, USA) and run under Linux (Version 2.6.32-5-amd64). Reconstructed fMRI data were analyzed using AFNI software (<http://afni.nimh.nih.gov/>) and related plug-ins (Cox, 1996). For each participant's data, the three imaging runs were concatenated into a single time series and brain volumes were motion corrected for global head translations and rotations. BOLD data of each participant were smoothed with a 5 mm full-width at half-maximum (FWHM) Gaussian kernel and converted to percent signal change relative to baseline on a voxel-wise basis for each scan run. All anatomical and functional imaging data were transformed into standardized Talairach coordinate space (Talairach and Tournoux, 1988). In a second-level analysis, participant data were combined to determine group-averaged activations for each condition and differences in the BOLD responses between conditions were examined (e.g. People > Things; Things > People).

For whole-brain correction, the AFNI plug-in AlphaSim was used to determine an appropriate cluster threshold. Applying a minimum cluster size of 4935 $\mu$ l (280 voxels), together with  $p < 0.025$  voxel-wise t-test, yielded a whole-brain correction at  $\alpha < 0.025$  for pairwise comparisons. Conjunction analyses were then performed to reveal only the regions of overlap between two sets of pairwise comparisons. This was done by taking the individual-voxel

thresholded ( $p < 0.025$ ) and cluster-corrected ( $\alpha < 0.025$ ) group activation map from four contrasts and merging the positive contrast components ( $[\text{People} > \text{Grey}] \cap [\text{Things} > \text{Grey}]$ ;  $[\text{People} > \text{Things}] \cap [\text{People} > \text{Grey}]$ ;  $[\text{Things} > \text{People}] \cap [\text{Things} > \text{Grey}]$ ). The resulting conjunction maps show activation in regions where both positive components are significant at  $p < 0.025$ . For visualization, activation data was projected onto surface models using SUMA (Saad et al., 2004).

To determine the exact locations of some activation clusters and create the histograms in Figure 4-5, a region of interest (ROI) analysis was performed. Analyses were carried out using ROIs based on combined functional and anatomical criteria. Specifically, ROIs were identified from the group t-statistic images for the conjunction analyses and then masked by anatomical ROIs pulled from the Talairach atlas within AFNI. The resultant masks were used on individual participant data to determine the interpretation condition effects on percent MR signal change in each region.



## 4.4 Results

A whole-brain analysis was performed to highlight activation differences between the two conditions. Figure 4-1 shows activation for People > Things (yellow) and Things > People (light blue). Tables 4-1 and 4-2 list the regions of activation for People > Things and Things > People, respectively. Robust activation was elicited over mainly visually sensitive brain regions, as well as large regions of frontal cortex, particularly for Things > People. The pairwise contrasts were set to an individual voxel probability threshold of  $p < 0.025$  and cluster corrected for multiple comparisons to yield a whole-brain correction at  $\alpha < 0.025$ . Of greater interest, however, was where both conditions showed responses that were greater than the blank grey screen, and where each condition was greater than both the grey screen and the opposing condition. Therefore, conjunction analyses were first used to identify where activation patterns to both visual stimulation conditions overlapped relative to the grey background, which served as an additional check for robustness of overall activation (Figure 4-2). As seen in the individual contrasts between conditions, the conjunction analysis also indicated that large regions of visually sensitive cortex and regions of frontal cortex were activated during the tasks, indicating that the participants were clearly engaging in a detailed analysis of the scene. Tables 4-1 and 4-2 list the regions of activation for People > Grey and Things > Grey, respectively.

A second conjunction analysis returned only the regions where the response to People was greater than both the blank grey screen, and the Things condition. Figure 4-3 shows activation to the individual contrasts of People > Things (yellow) and People > Grey (orange), as well as the overlap between the two contrasts (green). A similar conjunction analysis was also performed for the Things condition. Figure 4-4 shows activation to the individual contrasts of Things > People (light blue) and Things > Grey (light pink), as well as the overlap between the two contrasts (purple). The location and size (in number of voxels) of significant activation clusters specific to the People condition ( $[People > Grey] \cap [People > Things]$ ) and the Things condition ( $[Things > Grey] \cap [Things > People]$ ) are shown in Table 4-3. (Note: Although a cluster size minimum of 280 voxels was set for each pairwise comparison, these large clusters were often broken up during conjunction analyses and only the areas of overlap between two sets of pairwise comparisons were kept. The cluster sizes listed in Table 4-3 refer only to the regions of overlap remaining post conjunction analysis, and thus may be smaller than 280 voxels.)

Lastly, Figure 4-5 presents the significant activation clusters specific to the People condition ( $[\text{People} > \text{Grey}] \cap [\text{People} > \text{Things}]$ ) and the Things condition ( $[\text{Things} > \text{Grey}] \cap [\text{Things} > \text{People}]$ ) together on the same set of inflated brains. To determine the amount of BOLD percent signal change within different regions (histograms in Figure 4-5), post-hoc ROI analyses was performed, where ROIs were defined initially by group functional data and then anatomically based on the Talairach atlas regions within AFNI.

Results of the second conjunction analyses ( $[\text{People} > \text{Grey}] \cap [\text{People} > \text{Things}]$ ) showed that responses to the People condition were lateralized to the right hemisphere, with significantly greater activity than both the grey screen and the Things condition in the right superior temporal sulcus and superior temporal gyrus, which we refer to collectively as right superior temporal cortex, as well as in right middle temporal gyrus (Figure 4-5, green).

The conjunction analysis between  $[\text{Things} > \text{Grey}] \cap [\text{Things} > \text{People}]$  identified significantly greater activation to Things in a large number of regions (Figure 4-5, purple); some clusters were very large (see Table 4-3) and spanned several brain areas, but were identified with the help of both cluster and ROI analyses. These regions included bilateral structures such the superior frontal, middle frontal, medial frontal, inferior frontal and precentral gyri, the inferior and superior parietal lobules, the precuneus, and the middle occipital, fusiform, parahippocampal and lingual gyri. Activity was also present in right cingulate, left thalamus / pulvinar cortex, right cerebellum, right caudate, left insular cortex, and left inferior temporal gyrus.

## **4.5 Discussion**

The main findings from this study were that social and non-social interpretations of the same set of complex visual scenes generate different brain activation patterns. Most notably, the right middle and superior temporal cortices were preferentially activated by social interpretations of the manipulated TAT images. The different brain activation patterns observed for social and non-social interpretations are discussed in turn below.

### **4.5.1 Socially Relevant Interpretations**

Successful social interaction relies on the brain's ability to process information in the social domain correctly. The network of brain regions believed to be responsible for social and emotional cognitive processing consists of numerous sites of activation including frontal, limbic, and temporal regions (Allison et al., 2000; Carr et al., 2003; Iacoboni et al., 2004; Amodio and Frith, 2006). In the current study, when participants mentally evaluated the manipulated TAT images based on people in the scenes, including implied actions and their consequences, potential relationships with one another, and underlying mental states, we observed a refined right lateralized pattern of responses in the middle and superior temporal cortices. Importantly, these were the only brain regions preferentially activated during socially relevant interpretations.

Activity in middle and superior temporal cortices has previously been associated with socially relevant tasks, particularly when viewing images of faces and facial expressions of emotion (Puce et al., 1995; Puce et al., 1996; Kanwisher et al., 1997; Puce et al., 1998; Streit et al., 1999; Golarai et al., 2004). These areas do not just respond when viewing single images of faces, but also during face-to-face conversations (Suda et al., 2010), indicating their relevance to real-world social interactions. Faces, however, are not the only medium for emotional and social signals; the body in its entirety is able to convey social information, including emotion-related action intentions (van de Riet et al., 2009). By integrating facial expression with body positioning, we can generate potential reasons for, and responses to, an observed person's social and emotional behavior and intentions (de Gelder, 2006). Such methods would have been necessary in the present study in order for participants to create their mental descriptions of each social scene based on people. Eye data collected during the People condition confirmed that

participants were viewing the faces and bodies of the depicted individuals as well as moving back and forth between them (see Chapter 3). The activity we observed in right middle and superior temporal cortices to the People condition can in part be attributed to this process of extracting social information from faces and bodies and assimilating it in order to interpret the dynamics of a social scene.

The absence of People-specific activation in both the medial prefrontal cortex (MPFC), an area which has been well documented as playing a role in theory of mind reasoning (Frith and Frith, 1999), and the fusiform gyrus (specifically the fusiform face area), a region often activated during face perception tasks (Puce et al., 1995; Puce et al., 1996; Kanwisher et al., 1997; McCarthy et al., 1997), was unexpected. One explanation for a lack of MPFC activation in the People condition could be due to this brain region having a high baseline metabolic activity at rest (Ingvar, 1979; Raichle et al., 2001), which has been attributed to spontaneous self-generated mental activity and overlaps with the neurobiological signature of social cognition (Ingvar, 1985; Schilbach et al., 2008). If in our natural resting state we generate mental activity related to ourselves or others, then our task for the People condition, which essentially asks participants to maintain this state, may not lead to any significant change in MPFC activity levels. This notion is supported by the clusters of activity found in medial frontal cortex during the Things condition but not during the People condition. Another possible reason for the lack of MPFC activity may be because many of the experiments that have shown MPFC activation utilized tasks requiring participants to make explicit comparisons between or judgments of another person's emotional states or actions (Gusnard et al., 2001; Mason et al., 2004), which was not the focus of the present study. Activity in the fusiform, on the other hand, was observed during both conditions compared to rest (grey screen; see Figure 4-2), but the activation in this region during the People condition did not survive a further conjunction analysis designed to look at activation to People relative to both Things and the grey screen. It may be that any activity in the fusiform related to faces canceled out, as faces were present in all images (and thus in both interpretation conditions) and could have been attended to or fallen on the retinas of participants even if they were not intentionally fixated (Brefczynski and DeYoe, 1999; Reddy et al., 2004). Objects in the scene, though, would likely not play a role in the participants' social scenarios and indeed were fixated less; hence the only significant fusiform activity was that seen in response to objects during the Things condition.

The activity we found in right superior temporal cortex in response to the People condition may reflect participants' mental process of extracting social information to interpret the images. Specifically, the activity we observed in the People condition was likely the result of complex integrative processes, including using body language and scene context to infer the intentions, goals, and desires of the depicted people and incorporating these intentions into an appropriate interpretation of the illustrated social situation. In support of this are studies reporting activity in STS in response to static images that reflect the perception of potential movement or implied motion (Kourtzi and Kanwisher, 2000; Senior et al., 2000; Haxby et al., 2002), as well as to theory of mind cartoons and stories (Gallagher et al., 2000). Such findings indicate the sensitivity of the STS to socially relevant stimuli and especially those that signal human intentions. The results of our People condition point to the right superior temporal cortex as being responsible for incorporating social information in ways that will be useful for mentalizing about others and utilizing such information for generating descriptions of people and their intended actions within a scene. The right superior temporal cortex activation we observed provides further evidence that this region is where social information from faces, bodies, and scene context is both compiled and assimilated, acting as a social information processing "hub" of the brain.

#### **4.5.2 Non-Social Interpretations**

In the present study, identical scenes were interpreted based either on their social or non-social features. While the social interpretation required participants to investigate the people in the scenes, the non-social interpretation involved the realistic task of attending to objects and mentally describing their related properties (Things condition). The non-social interpretations produced an activation pattern that was very different from the brain regions preferentially activated by social interpretations. For one, activity during the Things condition was widely spread over many regions, unlike the focal activity in superior and middle temporal cortices observed for social interpretations. Interestingly, the greater activation in ventral visual regions in response to objects embedded within a complex scene is similar to activation previously reported for objects presented in isolation (e.g. Kohler et al., 1995; Malach et al., 1995; Martin et al., 1995; Martin et al., 1996; Aguirre et al., 1998; Ishai et al., 1999). We also found areas of

activity in occipitoparietal and dorsal occipitotemporal cortex, which have been linked to visual object perception and are thought to play a role in everyday object cognition (Schendan and Stern, 2007). The distributed pattern of activation related to producing mental descriptions of objects in the scenes is also similar to previous studies showing information related to objects is not stored in a single location, but instead is dispersed across a variety of brain regions subserving the extraction of categorical knowledge related to object stimuli (Caramazza and Shelton, 1998; Chao et al., 1999b; Caramazza, 2000; Haxby et al., 2000b; Martin et al., 2000; Haxby et al., 2001; Carlson et al., 2003; Cox and Savoy, 2003; O'Toole et al., 2005). Our data add further support to the idea that object perception entails gaining access to this stored information, a process that is thought to occur automatically when we attend to an object (Martin and Chao, 2001; Capitani et al., 2003).

Furthermore, it has been argued that regions of prefrontal cortex, including IFG, are essential for tasks requiring attention to and selection of a subset of semantically relevant information from among competing sources, and for enabling flexible and context-sensitive responses (Petersen et al., 1989; Petersen et al., 1990; Cohen and Servan-Schreiber, 1992; Domb et al., 1995; Martin et al., 1995; Thompson-Schill et al., 1997). The current study illustrates that despite the presence of multiple categories of information in a scene, including the normally more salient social cues, a separate pattern of brain activity was produced in association with attending to the non-social object features within an image. Such findings suggest participants were able to visually isolate only the non-social objects within the scenes and then, once an object was viewed, the cortical networks necessary for processing object information were automatically engaged.

However, some of the observed activity during the Things condition may be due to increased attention or working memory processes related to participants trying to ignore irrelevant aspects of the scenes and increase their focus on relevant features. One such region is the posterior parietal cortex, which has been implicated in helping to maintain an active representation of task-relevant information (Kanwisher and Wojciulik, 2000; Beauchamp et al., 2001; Corbetta and Shulman, 2002; Astafiev et al., 2003; Schendan and Stern, 2007). Additionally, prior research on inhibition demonstrated increased activity in regions of frontal and parietal cortices similar to those found here including, middle and superior frontal gyri, and cingulate (Garavan et al., 1999; de Zubicaray et al., 2000; Menon et al., 2001; Rubia et al., 2001;

Garavan et al., 2002; Horn et al., 2003; Maguire et al., 2003; Mostofsky et al., 2003; Sylvester et al., 2003; Asahi et al., 2004; Fassbender et al., 2004; Kelly et al., 2004; Buchsbaum et al., 2005; Rubia et al., 2005; Wager et al., 2005). Thus, a portion of the activity identified in these regions may be the result of participants trying to ignore, via attentional suppression, the elements of the scenes (people) that are developmentally and / or evolutionarily of more interest. Despite this, we believe participants were still appropriately executing the task of attending to the non-social objects, and limiting their attention to other aspects of the scene, as evidenced by the increases in fixation number and duration in *things* AOIs during this condition.

Moreover, we found greater activity in inferior temporal cortex and parahippocampal gyrus during the non-social interpretation compared to both the grey screen and the social condition, areas that are critical for recognizing and processing objects. Lesion studies in macaque monkeys have shown that bilateral removal of the inferior temporal cortex leads to impairments in learning visual shapes as well as deficits in remembering information necessary for making visual discriminations between objects (Mishkin, 1954; Mishkin and Pribram, 1954; Dean, 1976; Holmes and Gross, 1984). In humans, lesions of inferior temporal cortices lead to a variety of agnosias, or the inability to recognize certain types of objects, depending on the exact location of the injury (Logothetis and Sheinberg, 1996; De Renzi, 2000). Parahippocampal cortex activity similar to that found in the present study has been associated with processing the geometric structure of scenes (Epstein and Kanwisher, 1998). For example, responses in this area increase to photographs of furnished and empty rooms but not to photographs of furniture arrays on a white background, indicating that parahippocampal activation depends on the geometry of a three-dimensional space as defined by background structures (Epstein and Kanwisher, 1998). Another study showed that parahippocampal activity is higher to objects that are strongly associated with a particular context than to random objects, pointing towards a potential role for this area in processing scene gist (Bar and Aminoff, 2003). Given that our stimuli were complex and coherent scenes with background structures (e.g. barn) that defined each scene, the activation in parahippocampal cortex present in the current study is consistent with participants viewing the objects in each image and perhaps relating them to one another to make sense of the scene.

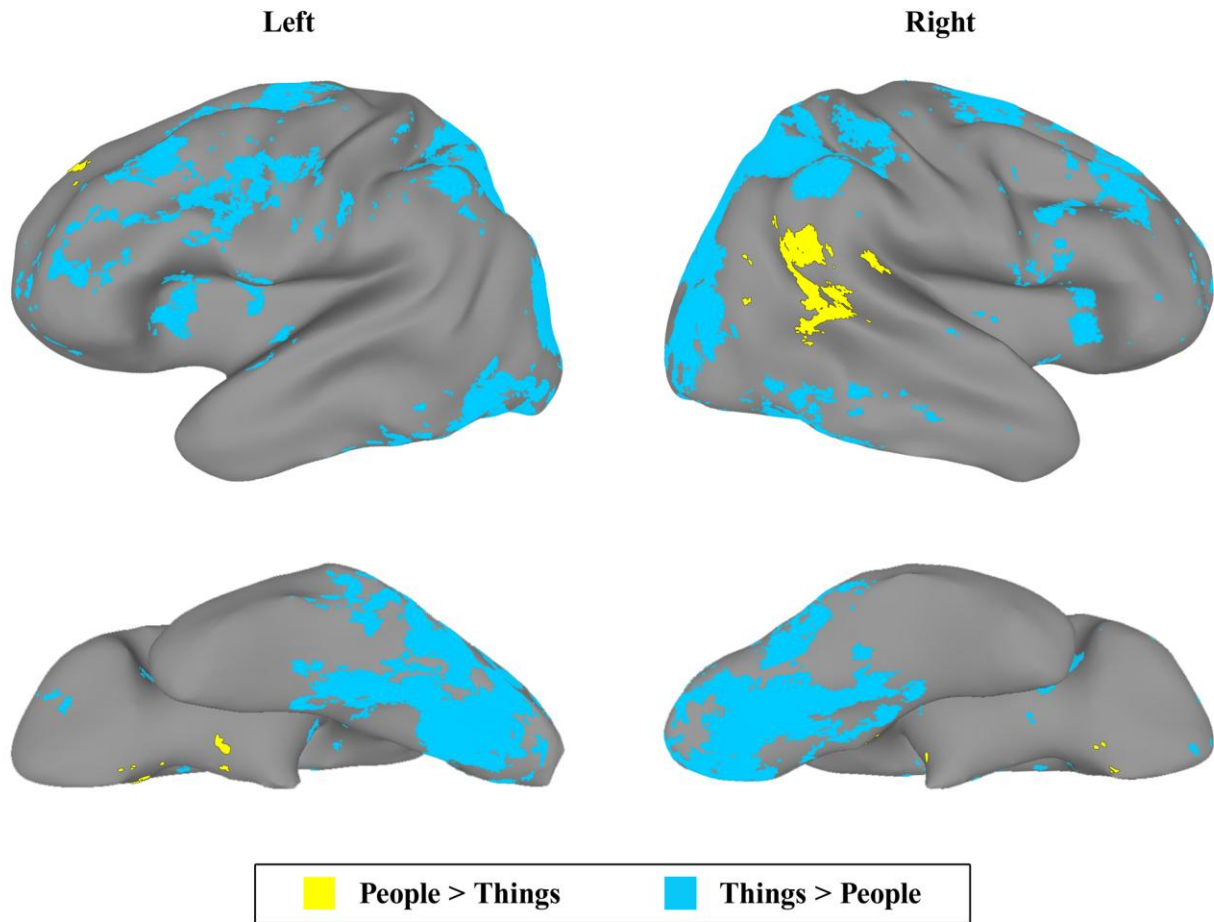
Our results from the non-social condition imply that similar activation patterns can be found regardless of whether objects are presented in isolation or amongst other objects in a complex scene.

### **4.5.3 Conclusions**

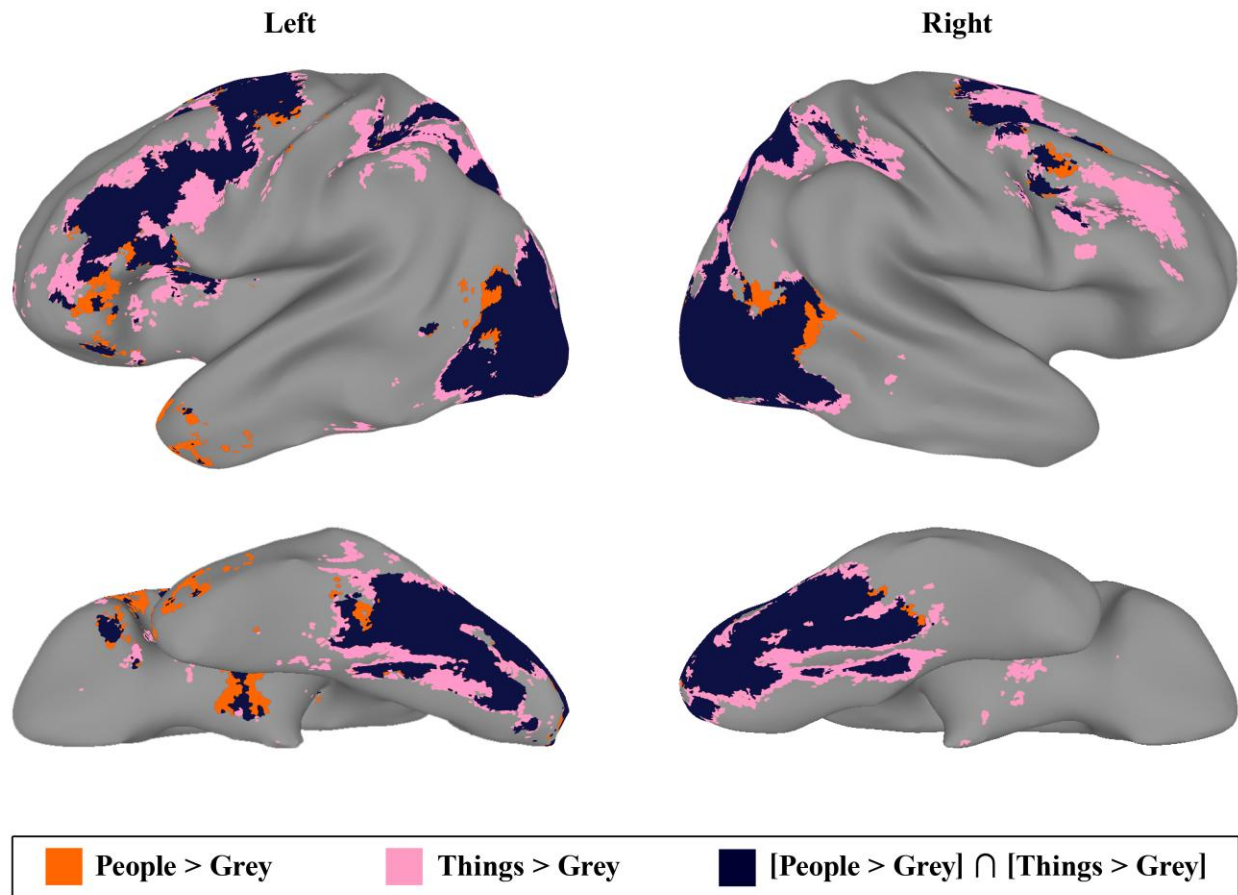
Summarizing, the present fMRI data demonstrate differential activation patterns in response to separate interpretations of identical sets of complex images. Interpreting these images from a social perspective preferentially activated the right middle and superior temporal cortices, while non-social interpretations produced activity in parahippocampal gyri as well as regions of frontal and occipitotemporal cortices. These findings highlight the superior temporal cortex as an important region for processing social information including the ability to identify and extract social cues from within a scene and apply them in order to decode and interpret complex social interactions. In addition, the results of the current study are in agreement with those of previous studies that presented separate stimuli for each category. An important conclusion from these findings is that multiple research questions as well as different levels of object or social processing can be examined using a single set of complex stimuli. Experiments with this type of design have the advantage of matching our natural environment more closely. For instance, although we may see the same room or building multiple times each day, how we attend to and processes that room or building may change depending on our current needs and goals.



## 4.6 Figures and Tables



**Figure 4-1.** Group brain activity to each condition projected onto lateral and ventral views of inflated brains made using SUMA cortical surface models ( $p < 0.025$ ,  $\alpha < 0.025$ , cluster-corrected). Regions where activation to People was significantly greater than to Things are displayed in yellow, while regions where activation to Things was significantly greater than the activation to People are shown in light blue.



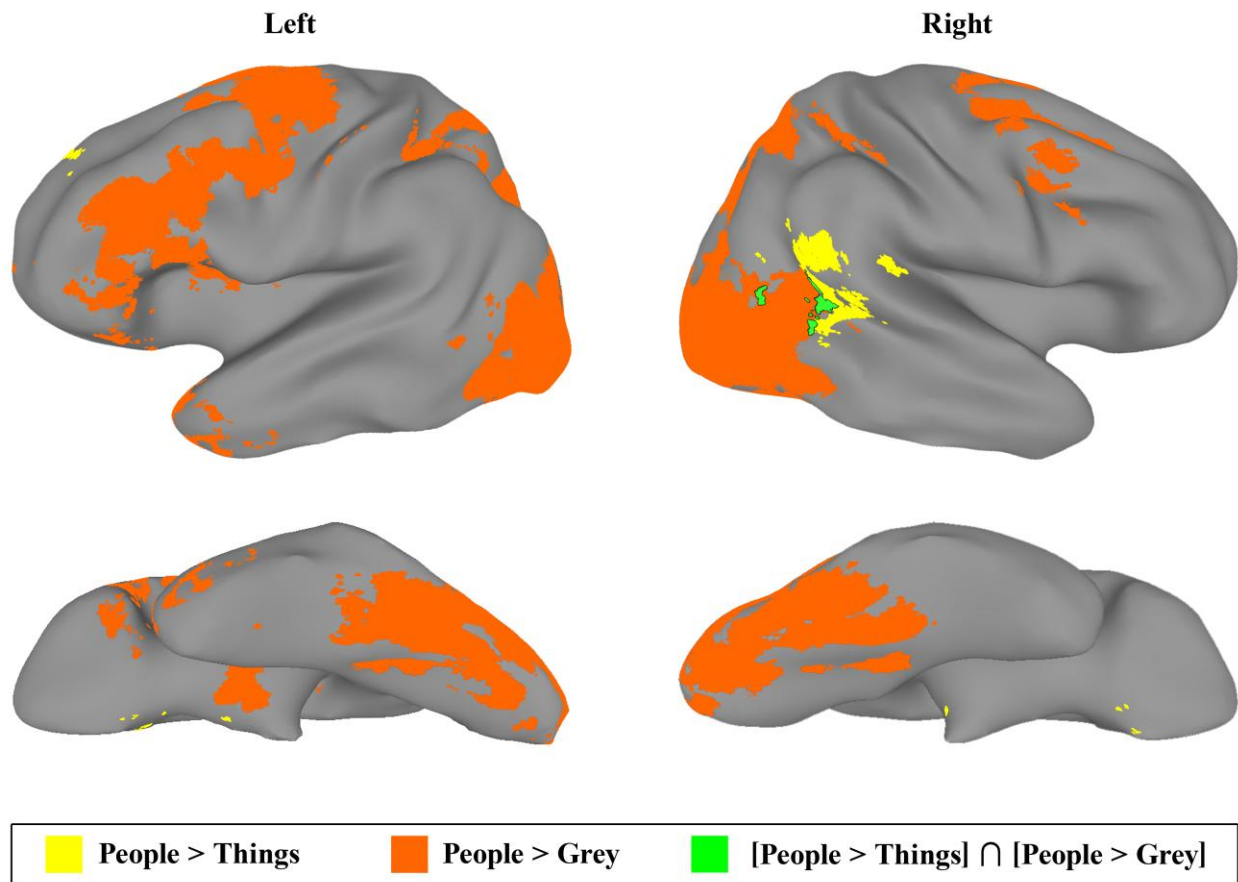
**Figure 4-2.** Group brain activity to both conditions versus rest. Regions where activation to People was significantly greater than to the blank grey screen (Grey, displayed during rest) are shown in orange, while regions where activation to Things was significantly greater than the blank grey screen are shown in light pink. Overlap between the two individual contrasts (displayed in navy blue) indicates the regions commonly activated by both conditions compared to rest. All activation is shown on the lateral and ventral surfaces of inflated brains made using SUMA cortical surface models ( $p < 0.025$ ,  $\alpha < 0.025$ , cluster-corrected for multiple comparisons).

**Table 4-1. Location and number of activated voxels to the People condition**

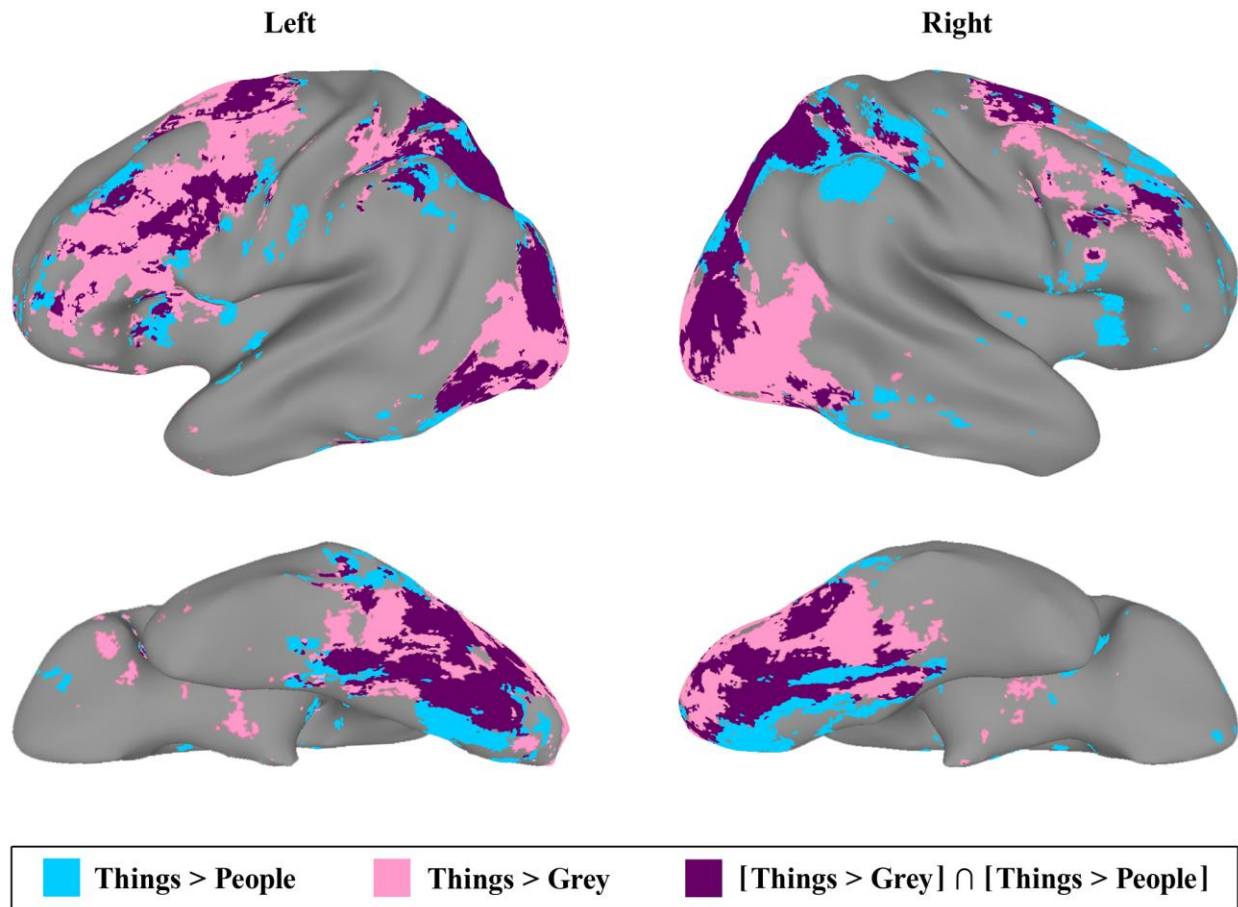
| Anatomical Location           | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|-------------------------------|-------------------------------------|-----|-----|------------------|
|                               | x                                   | y   | z   |                  |
| <i>People &gt; Grey</i>       |                                     |     |     |                  |
| Posterior cingulate           | 0                                   | -66 | 10  | 258467           |
| Left Fusiform                 | -23                                 | -95 | -18 | 587              |
| Right Precentral gyrus        | 39                                  | -10 | 67  | 370              |
| Left Middle frontal gyrus     | -31                                 | 59  | 6   | 324              |
| <i>People &gt; Things</i>     |                                     |     |     |                  |
| Right Superior temporal gyrus | 50                                  | -48 | 16  | 4084             |
| Left Medial frontal gyrus     | -5                                  | 46  | 12  | 1611             |
| Left Superior frontal gyrus   | -7                                  | 53  | 31  | 1532             |
| Left Anterior cingulate       | -1                                  | 5   | -8  | 522              |

**Table 4-2. Location and number of activated voxels to the Things condition**

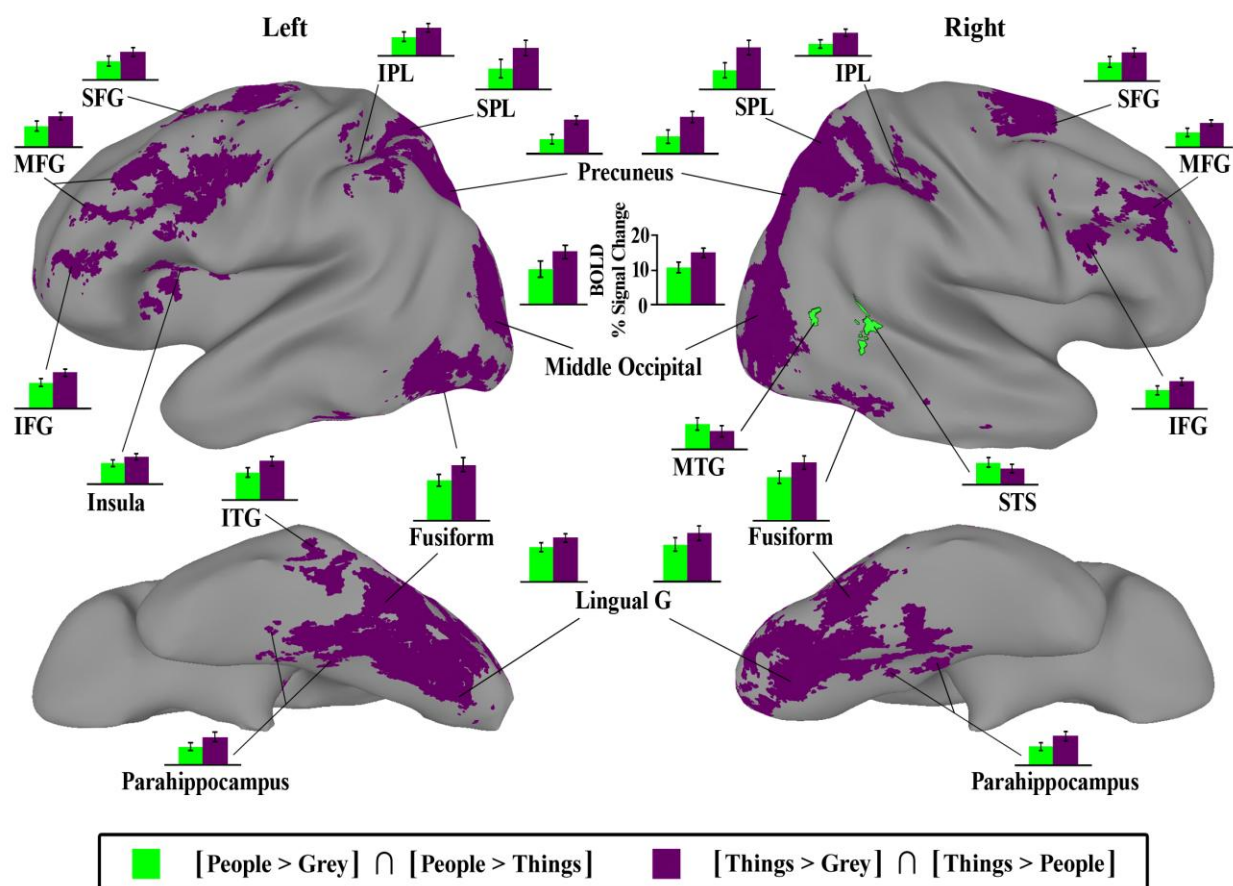
| Anatomical Location          | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|------------------------------|-------------------------------------|-----|-----|------------------|
|                              | x                                   | y   | z   |                  |
| <i>Things &gt; Grey</i>      |                                     |     |     |                  |
| Posterior cingulate          | 0                                   | -59 | 16  | 366250           |
| Left Inferior frontal gyrus  | -32                                 | 16  | -16 | 981              |
| Right Parahippocampus        | 24                                  | -2  | -15 | 779              |
| Left Middle frontal gyrus    | -34                                 | 56  | 6   | 641              |
| Right Middle temporal gyrus  | 75                                  | -10 | -7  | 498              |
| <i>Things &gt; People</i>    |                                     |     |     |                  |
| Precuneus                    | 0                                   | -63 | 30  | 204404           |
| Left Middle frontal gyrus    | -41                                 | 19  | 25  | 19884            |
| Right Middle frontal gyrus   | 32                                  | 26  | 29  | 19477            |
| Left Superior temporal gyrus | -67                                 | 11  | -8  | 2548             |
| Right Precentral gyrus       | 72                                  | 5   | 19  | 2186             |
| Right Middle frontal gyrus   | 56                                  | 46  | 8   | 1950             |
| Left Thalamus / pulvinar     | -18                                 | -27 | 6   | 1633             |
| Right Middle frontal gyrus   | 32                                  | 63  | 10  | 1091             |
| Right Superior frontal gyrus | 34                                  | 72  | -2  | 1017             |
| Right Cerebellar tonsil      | 28                                  | -58 | -33 | 912              |
| Right Medial frontal gyrus   | 10                                  | 57  | -18 | 693              |
| Left Middle frontal gyrus    | -48                                 | 47  | -6  | 651              |
| Left Superior frontal gyrus  | -44                                 | 58  | 19  | 416              |
| Right Thalamus               | 11                                  | -22 | 15  | 326              |
| Left Superior frontal gyrus  | -26                                 | 55  | -12 | 311              |



**Figure 4-3.** Group brain activity to the People condition projected onto lateral and ventral views of inflated brains made using SUMA cortical surface models ( $p < 0.025$ ,  $\alpha < 0.025$ , cluster-corrected). Regions where activation to People was significantly greater than to the blank grey screen are displayed in orange, while regions where activation to People was significantly greater than the activation to Things are shown in yellow. Overlap between the two individual contrasts is shown in green.



**Figure 4-4.** Group brain activity to the Things condition projected onto lateral and ventral views of inflated brains made using SUMA cortical surface models ( $p < 0.025$ ,  $\alpha < 0.025$ , cluster-corrected for multiple comparisons). Regions where activation to Things was significantly greater than to the blank grey screen are displayed in light pink, while regions where activation to Things was significantly greater than the activation to People are shown in light blue. Overlap between the two individual contrasts is shown in purple.



**Figure 4-5.** Group brain data showing regions preferentially activated by each condition. Patterns in green illustrate regions where responses to People were significantly greater than both the grey screen (displayed during rest) and the Things condition. Regions where responses to Things were significantly greater than the grey screen and the People condition are shown in purple. Histograms from selected activation clusters depict relative degrees of activation to each condition for each ROI in BOLD percent signal change (mean  $\pm$  standard error). All data are shown projected onto lateral and ventral views of inflated brains made using SUMA cortical surface models ( $p < 0.025$ ,  $\alpha < 0.025$ , cluster-corrected). Abbreviations: IFG, inferior frontal gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; Lingual G, lingual gyrus; MFG, middle frontal gyrus; MTG, medial temporal gyrus; SFG, superior frontal gyrus; SPL, superior parietal lobule; STS, superior temporal sulcus



**Table 4-3. Location and number of activated voxels for conjunction analyses**

| Anatomical Location                                   | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|---|-------------------------------------|-----|-----|------------------|
|   | x                                   | y   | z   |                  |
| <b>People &gt; Things <i>and</i> People &gt; Grey</b> |                                     |     |     |                  |
| Right Middle temporal gyrus                           | 50                                  | -55 | 10  | 60               |
| Right Superior temporal sulcus                        | 43                                  | -47 | 13  | 36               |
| Right Superior temporal sulcus                        | 42                                  | -49 | 16  | 17               |
| Right Middle temporal gyrus                           | 49                                  | -57 | 12  | 12               |
| <b>Things &gt; People <i>and</i> Things &gt; Grey</b> |                                     |     |     |                  |
| Left Precuneus  | 0                                   | -66 | 19  | 104987           |
| Left Medial frontal gyrus                             | -3                                  | -1  | 56  | 17155            |
| Left Inferior frontal gyrus                           | -38                                 | 9   | 24  | 11441            |
| Right Middle frontal gyrus                            | 41                                  | 20  | 28  | 4054             |
| Right Precentral gyrus                                | 72                                  | 5   | 16  | 1029             |
| Left Thalamus / Pulvinar                              | -21                                 | -26 | 3   | 567              |
| Right Cerebellar tonsil                               | 32                                  | -53 | -30 | 216              |
| Left Thalamus   | -10                                 | -10 | -3  | 172              |
| Right Caudate   | 16                                  | 11  | 9   | 122              |
| Left Inferior frontal gyrus                           | -28                                 | 26  | 2   | 115              |
| Left Precentral gyrus                                 | -53                                 | 1   | 44  | 111              |
| Right Cingulate                                       | 16                                  | 10  | 24  | 106              |
| Right Cingulate                                       | 10                                  | 20  | 37  | 91               |
| Left Precuneus  | -16                                 | -85 | 49  | 86               |
| Left Inferior frontal gyrus                           | -47                                 | 46  | 0   | 81               |



## **CHAPTER 5: General Discussion and Conclusions**

This chapter first summarizes the results across all experiments in terms of the objectives and hypotheses set out in Chapter 2. This is followed by sections that discuss the significance of the current findings in relation to previous studies, starting with the role of the superior temporal cortex, particularly the right STS in social processing. Next, the relationship between eye movements and brain activity and its importance for proper social functioning is discussed. Finally, the implications of these findings, suggestions for future studies, and general conclusions complete this chapter.

## **5.1 Summary**

The purpose of this dissertation was to explore the effects that social and non-social interpretations of identical complex images would have on the eye movement (Study 1, Chapter 3) and brain activity of humans (Study 2, Chapter 4). Examining how humans view, extract, and process social information has been the subject of increasing interest among investigators due to the prominent role social encounters play in our daily lives. Disruptions in these abilities have been identified in a variety of disorders, such as autism and schizophrenia, often resulting in a lack of social functioning and a decreased quality of life for these individuals. However, the mechanisms underlying the behavioral deficits and improper social information processing that occurs in these individuals have yet to be established. The findings presented herein point towards improper viewing strategies for social stimuli and / or an inability of the middle and superior temporal cortices to receive or process social information as potential factors. The experiments described in the previous chapters may serve as a framework, whereby hypotheses for the involvement of viewing strategy or faulty temporal cortex functioning in social cognition disorders may be tested. Moreover, the present results add to the depth of knowledge regarding how the eyes and brain work together to extract and integrate social and non-social information from a scene.

### ***Study 1: Is viewing strategy altered by how a complex scene is interpreted?***

To investigate whether social and non-social interpretations of complex images would alter viewing strategy, the eye movements of healthy participants were recorded using an infrared eye tracker while they were presented with static images depicting people involved in complex social situations. During the experiment, participants were instructed to interpret the images based on socially or non-socially relevant aspects of the scene. The results presented in Chapter 3 demonstrate that while the number and duration of fixations did not differ overall between conditions, the distributions of fixation numbers and durations within the scenes were different for each condition. These results support the hypothesis, showing that participants spent more time viewing the people in the images, especially their heads, during socially relevant interpretations of the images, whereas non-social interpretations were associated with fixations that were directed more towards objects. Although previous studies reported unique fixation patterns produced by asking participants different questions about a scene, these fixation patterns were not quantified or statistically compared. Further, the effects of social and non-social interpretations were not directly compared. The study presented in Chapter 2 provides a first report of statistically significant differences in the distribution of fixations for social versus non-social interpretations of the same scenes.

### ***Study 2: How do social and non-social interpretations of a complex scene affect brain activity?***

Many previous investigations of the brain's responses to social and non-social processing have used individual sets of stimuli for each category. Though useful, such studies do not reflect how the world is actually viewed. The environment is usually multifaceted, containing people, objects, and buildings, set against a variety of backgrounds. Therefore, the goal of the study presented in Chapter 4 was to explore the brain activity elicited to social and non-social interpretations of the same complex scenes. Results showed differential brain activity patterns preferential for each of the interpretations and pinpointed areas in the middle and superior temporal cortices that are associated with interpreting social intention information within a scene, and dissociated this network from those involved in object recognition, including regions

of inferior temporal cortex, fusiform, and parahippocampus. The results of Chapter 4 are some of the first to show that the patterns of activity obtained using a single set of stimuli are similar to those reported in response to isolated presentations of stimuli. Further, these results demonstrate that the right superior temporal cortex is a central region recruited for viewing and interpreting socially salient signals from complex scenes and suggests it is an essential area for mentalizing about others, a skill critical for proper social functioning.

The data presented in this dissertation support previous studies implying that social information requires deeper processing compared to non-social information, as evidenced by the increase in fixation number and duration directed to socially salient areas, particularly the head region of the body, compared to non-social interpretations where the focus is directed more towards inanimate objects and the background. Additionally, this work has led to the conclusion that at least one role of the right superior temporal cortex is to act as a central processing ‘hub’ for social information, and is especially important for mentalizing about others in order to decode and interpret their behavior. Taken together, data from both studies suggest a complex relationship between eye movement and brain activity patterns that, if faulty, may lead to impairments in viewing and processing social stimuli.

## 5.2 Discussion

### 5.2.1 Social Processing, Mentalizing, and the Superior Temporal Cortex

The superior temporal cortex is involved in different aspects of social cognition and language processing and is the most responsive when presented with stimuli that have communicative significance. It has been proposed that this region is able to take the input from both of these domains and separate them into interpretable units in order to extract meaning from them (Redcay, 2008). In the social domain, it is thought that the STS is responsible for evaluating eye-gaze direction, facial expressions, body movements, and other biologically relevant stimuli to determine the social communicative intentions of others (Allison et al., 2000). Pelphrey and Morris (2006) have reported that the social stimuli that produce activation in the STS fit generally into the category of biological motion or the ‘visual perception of a biological entity engaged in a recognizable activity’. However, the motion need not be explicit, as responses in the STS are observed to socially relevant static images and images that imply motion (Kourtzi and Kanwisher, 2000; Senior et al., 2000; Jellema and Perrett, 2003; LaBar et al., 2003). A necessary component for eliciting STS activity appears to be the social content of a stimulus, as little to no activation occurs to random motion or to static non-socially relevant stimuli (Beauchamp et al., 2002; Redcay, 2008).

In the results from Chapter 4, significantly greater superior temporal cortex activity was observed for the social interpretation condition over the non-social condition. This observation along with the use of modified TAT images as stimuli together support that superior temporal cortex is sensitive to stimuli only when interpreted in a way that is socially significant. This work provides evidence that superior temporal cortex is involved in scene processing in order to identify *social* elements and extract meaning from them, since activation in this region was preferential for the People condition compared to when participants viewed the same modified TAT images but were instructed to identify and describe non-social objects. The right superior temporal cortex activity being selective for the social condition also suggests that the presence of social content alone is not what drives activity in this region. Rather, activation of right superior temporal cortex may be due to the act of using the social information to mentalize about others, or to infer their thoughts and beliefs in order to better understand their behavior. This notion is supported by previous studies that have reported greater activation in STS when participants

infer the goals and intentions from another person compared to simply perceiving biological motion (Frith and Frith, 2003; Redcay, 2008).

Neuroimaging studies in humans have implicated bilateral MPFC, as well as the STS (see Figure 1-5), in tasks relevant to mentalizing (Frith and Frith, 2003; Gallagher and Frith, 2003). The results of Chapter 4 showed middle and superior temporal cortex activity that was selectively activated when participants mentalized about the people in the images (People condition), but did not show activity in MPFC during this condition. This observation suggests that while activity in both regions may occur simultaneously during some social tasks, the middle and superior temporal cortex likely perform a separate function in the social processing network than the MPFC. In support of this idea, a study by Hampton et al. (2008) demonstrated that MPFC and STS fulfilled different roles when participants were engaged in an interactive strategic game. By combining fMRI data, behavioral responses, and computational modeling, the researchers found that activity in MPFC correlated with the predicted reward a participant associated with a decision during the game while activity in the posterior STS correlated with the degree of influence the participant believed they had over their opponent. Hampton and colleagues (2008) speculate that the signals in MPFC may have helped guide participants' choices during the game, whereas signals in STS may have modulated participants' 'influence expectations' based on the 'actual outcomes [they] experienced' (Hampton et al., 2008). In other words, MPFC potentially acts as a social decision maker while STS may be more involved in interpreting the thoughts of others in order to gauge 'where we stand' in a given circumstance and adjust our behavior accordingly.

Other studies support this role of MPFC in social decision-making, particularly those requiring participants to make explicit comparisons or judgments of the emotional states or actions of others. Two examples are a study by Gusnard et al. (2001), where participants were asked to judge whether an image evoked pleasant or unpleasant emotions in themselves, and a study by Mason et al. (2004), where participants judged whether a series of actions could or could not be performed by a person (versus a dog). Both experiments found increased MPFC activity, which could be interpreted as being related to making structured, socially oriented evaluative decisions or judgments about others, rather than to mentalizing per se. Because the experimental paradigm presented in this dissertation directed participants to think about and describe the thoughts and behavior of the people in the scenes and did not ask participants to

make any explicit social judgments regarding those scenes, this therefore may explain why activity was observed in right middle and superior temporal cortices but not MPFC during Study 2.

The results of this work and previous studies support that the superior temporal cortex is not just important for identifying intentional actions but also participates in the integration of such actions with social context and as such is sensitive to the environmental or cognitive sources that inform this context (Pelphrey et al., 2003; Wyk et al., 2009). The activation in right middle and superior temporal cortices reported in Chapter 4 provides further evidence that these regions are where social information from faces, bodies, and scene context is both compiled and assimilated when analyzing a social scene. Activity in the superior temporal cortex is not simply due to identifying and assembling social information, but is essential for extracting meaning from social cues and permits appropriate application of that knowledge during social situations. In accordance with this idea is a recent fMRI study investigating responses to a strategic game task, which demonstrated that activity in the posterior STS was correlated with participants' previous and future cooperation, which in turn was related to their interpersonal ties (Fahrenfort et al., 2012). Furthermore, individual differences in STS activation predicted individual differences in prosocial behavior in the game. These results imply that the STS plays a role in continually monitoring our relationships and updating our knowledge regarding past interactions with others, which may help shape how we interact with those individuals in the future. Moreover, STS activity may be important for motivating humans to engage in social behavior (Fahrenfort et al., 2012). Supporting this notion are studies indicating STS abnormalities in autism, a disorder known to be associated with impairments in social behavior (Castelli et al., 2002; Pelphrey et al., 2005).

Interestingly, asymmetries in superior temporal cortex have been noted in the adult brain, including a deeper STS in the right versus the left hemisphere, especially in the posterior region (Ochiiai et al., 2004; Van Essen, 2005). Even more fascinating are recent neuroimaging studies reporting earlier gyrification on the right side of the brain in preterm human infants, with both preterm and full-term infants exhibiting a deeper right STS than left STS (Dubois et al., 2008; Dubois et al., 2010; Hill et al., 2010; Glasel et al., 2011). Together these studies imply that a deeper right STS is an important feature of the human brain across the lifespan (Glasel et al., 2011). Though the exact purpose of anatomical asymmetries remain speculative (e.g.

Markowitsch and Tulving, 1994; Van Essen, 1997), it is probably not a coincidence that there is a similar functional asymmetry in STS activity during theory of mind and biological motion perception tasks (Pelphrey and Carter, 2008; Wyk et al., 2009).

In sum, the superior temporal cortex is paramount for identifying social cues, inferring the thoughts and mental states of others, and implementing this knowledge during social interactions. Based on evidence from anatomical connectivity studies in monkeys showing that the STS has connections to multiple regions of the brain (Seltzer and Pandya, 1978, 1989b, a, 1994), Frith and Frith (2001) postulated that these connections and the location of the STS within the brain - halfway between the ventral and dorsal streams - make the STS ideally situated for acting as the link between these streams by associating objects with their respective action information. The results of the People condition in Chapter 4 point particularly to *right* superior temporal cortex as being responsible for collecting socially salient information, extracting its meaning, and using this knowledge to generate socially relevant descriptions of people and their actions. The work presented in this dissertation adds to the growing body of literature implicating that the right superior temporal cortex acts as the interface between socially relevant object and action information, serving to integrate elements from both streams together in order to help us infer and predict the mental states and behavior of others during social interactions.

### **5.2.2 The Link between Eye Movement and Cognition**

The visual environment contains a wealth of information, only some of which is actually used at a given instant in time. Critical to the process of selecting relevant information while ignoring irrelevant signals or noise in the environment, is attention. Selective attention is also necessary due to the fixed amount of energy available to the brain and because of the high-energy cost associated with cortical computations. By ignoring the unimportant aspects of a visual scene, the representations of the relevant regions can be enhanced, and allows us to perceive and interpret only the parts of the environment that are biologically or evolutionarily relevant, factors which are essential for successfully guiding human behavior (Brefczynski and DeYoe, 1999; Carrasco, 2011).

One of the principal ways attention can be allocated is by directing the eyes through a sequence of locations in the visual field. This type of attention is called overt attention, and



permits different images within the environment to fall on the fovea, the region of the eye with maximum acuity of vision. Another type of attention, called covert attention, can be directed to areas in the periphery without moving the eyes (Carrasco, 2011). In general, it is thought that covert attention precedes eye movements and the direction of overt attention (Rizzolatti et al., 1994; Deubel and Schneider, 1996).

Because of this link between eye movements and attention, it has been suggested that eye movement data can indicate the cognitive processes underlying various tasks (see Liversedge and Findlay, 2000). The association between eye movements and cognition has been illustrated in several activities of daily life such as driving, playing table tennis (Land and Furneaux, 1997), reading (Rayner, 1998; Hyona and Nurminen, 2006), or problem solving (Grant and Spivey, 2003; Thomas and Lleras, 2007). The results of experiments recording participants' eye movements as they engage in problem solving tasks show that successful problem solvers make paths with their eyes that reveal the solution. For example, several studies have tracked participants' eye movements as they viewed adapted versions of Duncker's radiation problem (shown in Figure 5-1) given the following instructions (Duncker, 1945; Grant and Spivey, 2003; Thomas and Lleras, 2007):

Given a human being with an inoperable stomach tumor, and lasers which destroy organic tissue at sufficient intensity, how can one cure the person with these lasers and, at the same time, avoid harming the healthy tissue that surrounds the tumor?

The correct solution involves firing several low-intensity lasers from various locations outside the tumor. Each laser on its own is too weak to damage the surrounding healthy tissue, but when combined, the lasers have enough intensity to destroy the tumor. Eye tracking data recorded as participants' performed this task showed that the participants who made more eye movements in a triangular in-and-out pattern (i.e. moved their eyes from the outer area, across the skin to the tumor area, and then back out again) were more successful at solving the problem than participants that made fewer in-and-out movements. This in-and-out pattern of the eyes actually draws paths reflecting the convergence of multiple lasers from different outer areas onto the tumor. In other words, participants' eye scan paths acted as an embodied physical mechanism (Barsalou, 1999) that guided participant's cognitive processes toward how to correctly solve the problem (Grant and Spivey, 2003; Thomas and Lleras, 2007).

Viewing movies has also been shown to affect both eye movement and brain activity, but in a more controlled way. Filmmakers are able to direct viewers' attention and eye movements by altering how a scene is lit, composed, or framed. Hasson et al. (2008) showed that watching a professionally filmed and edited movie resulted in cohesive eye movement patterns, with all viewers tending to fixate on similar objects within each shot at about the same time. Eye movement during unstructured videos however was much more variable across participants, which likely also induced the observed increase in the variability of brain responses across viewers. The authors suggest that variability in brain activity may affect the interpretation of a given scene and subsequent scenes as well. Together, their data imply that the ability to select and process relevant information within a scene is necessary for successfully interpreting that scene and perhaps even the environment as a whole. Furthermore, these results highlight that by recording eye movements and brain activity simultaneously, complementary information regarding the cognitive and emotional effects of a scene can be obtained (Hasson et al., 2008).

Similar to the study by Hasson and colleagues, the eye movement and brain data presented in this dissertation were collected simultaneously. In doing so, we were able to confirm participants were performing the task without the need for a button response or other behavioral task that would produce brain activity unrelated to the task of interest. Additionally, as eye movements are usually the physical manifestation of cognitive shifts of attention, collecting eye movement data would provide a 'map' of scene regions participants' selectively attended to during each interpretation. The results of Study 1 (Chapter 3) and Study 2 (Chapter 4) demonstrated that each interpretation condition differently affected participant's eye movement and brain activation. Although causation cannot be determined definitively, it's likely that top-down processes activated by task instruction initially led participant's eyes to focus on scene regions most informative for each condition and in doing so activated brain networks associated with processing those aspects. Our findings support the idea that even when viewing and interpreting every day scenes, eye movement patterns both reflect what we are thinking and can influence our thoughts as well.

Fixation patterns can also reflect the difficulty of a particular task. For instance, as visual search tasks increase in difficulty, so does the duration of fixations (Hooge and Erkelens, 1996). This observation insinuates that when faced with a difficult or complex task, increasing fixation durations ensures increased allocation of attention and brain resources for processing the relevant

information. The eye movement data in Chapter 3 did not show significant differences in the mean fixation durations to each condition as a whole, indicating that neither condition was particularly more difficult than the other condition. However, *where* participants spent the most time viewing within a scene was different, with longer fixations to people occurring during the social condition, and longer durations to objects occurring during the non-social condition. These findings assert that in order to interpret the scene as either social or non-social, increased attention was needed at these locations. Alternatively, increased attention at these locations may have helped fuel the complex brain processes associated with each interpretation.

While fixations are able to signal many aspects of attention and cognition, determining attentional workload though is a bit more difficult as no direct measurement method is available. However, one potential indicator is pupillary dilation, or pupil size. Comparison of pupil diameter between different tasks is one way to evaluate whether the tasks were equivalent in attentional workload (Kahneman, 1973; Janisse, 1977; Beatty, 1982; Hoecks and Levelt, 1993). Although pupil size can also signal low-level stimulus differences such as contrast, the data presented in Chapter 3 indicated no difference in mean pupil size between the social and non-social conditions. These results imply that our stimuli were well equated for luminance and contrast and that our two interpretation conditions were well balanced for the amount of attention participants had to dedicate to each. This is further supported by the lack of a significant main effect of Condition for both the number and duration of fixations, which suggests participants did not direct attention more during one condition compared to the other, the difference between the conditions instead was related to *where* participants directed their attention within the scenes. The different fixation patterns observed to each condition was also reflected in the brain activation patterns of participants for each condition. Although the correlation was not directly measured, the social interpretation was associated with increased fixations to people and brain activity in right superior and middle temporal cortices, while the non-social condition was associated with fixations directed more towards objects in the scenes and brain activity in parahippocampus, fusiform, and inferior temporal gyrus. Together, the data presented in this dissertation support the notion that eye movements and brain activity are intertwined.

### **5.2.3 Limitations of the Current Paradigm and Ideas for Improvement**

The paradigm and results of the studies described in Chapters 3 and 4, although interesting and novel, are not without a few limitations. For one, even though an attempt was made to create a control condition during which participants were to view a series of crosshairs overlaid onto each image (Crosshairs condition), unfortunately, both the eye movement and brain activation data for this condition did not demonstrate the qualities of a good control.

Consequently, the data for the Crosshairs condition was not included as part of the final analyses in Chapters 3 and 4 (for results and discussion of the eye movement and brain activation data to this condition see Appendix Sections A.3 and A.4, respectively). A main issue during data collection and analysis of the Crosshairs condition was the location of the crosshairs on the images. Their placement near the outer edge of the images made it difficult for the eye tracker to track and detect the eye movements and fixations in these regions. Additionally, participants were instructed to move from crosshair to crosshair in no particular order and were not told specifically to pause and fixate on each crosshair, which may have led to the decreased number of fixations detected in this condition. Brain activation to Crosshairs was more robust than the activation to the other two conditions, perhaps reflecting the more forced nature of the task and the increased number of saccades participants made during this condition. As a result, much of the activation to the People and Things conditions was subtracted out when contrasted with the Crosshairs condition, making data interpretation for the three conditions problematic.

Subsequently, the grey blank screen that was displayed during rest was determined to be a better control for basic attention and visual activity than the Crosshairs condition. Future experiments using this paradigm would benefit from the addition of a free-view condition, where participants are able to explore and think about each scene in a natural way. A free-view condition would provide not only a control for eye movement and attention, but would also serve as a way to determine whether our natural eye movements and thoughts when viewing complex scenes are more closely related to those observed during the social or non-social condition.

A second limitation to Studies 1 & 2 is that participants were not debriefed after the experimental sessions in order to assess how they performed the task. Without having asked participants to report what they had been thinking about for each image, even with the eye movement data we cannot know to what degree they were mentalizing about the people in the images (or thinking about the objects). Brain activation data suggests that there was at least some

mentalizing given the observed activation in right superior and middle temporal cortices, however the robust responses to the Things condition indicates that it may have been the more difficult task to perform. While this would be the logical conclusion for the more expansive brain activation pattern for Things, without participants' statements regarding the validity of this conclusion, we can only assume this is the case based on the data we observed. Future studies of this nature should include a post-fMRI session that would allow participants to describe in writing the social and non-social stories or thoughts that they were able to produce for each image while in the scanner. It may also be useful to have participants rate or describe the level of difficulty they experienced when generating the interpretations for each scene. Having participants' notes regarding their stories, thoughts, and perceived difficulties would be helpful in confirming if one type of interpretation was more difficult to perform than the other, as well as if there were certain scenes that were particularly difficult to interpret and perhaps should have been eliminated from analysis.

Another limitation is that the current analysis procedure is not sufficient to establish definitively whether participants' eye movements were the cause or result of the observed brain activation. Further studies are needed to determine if the eye movements produced during social interpretations of scenes drive brain activity, or if the brain activity precedes and / or influences eye movements to social scenes. Interestingly, investigations on theory of mind processing in blind individuals have demonstrated that both sighted and congenitally blind adults activate similar regions of cortex, including temporal parietal junction, MPFC, and STS (Bedny et al., 2009). These data imply that the neural mechanisms for theory of mind depend on innate factors and experiences, and that these experiences need not be limited to one modality (e.g. vision). Furthermore, being blind does not appear to hinder the development of the neural representations responsible for understanding other people's experiences of seeing. Bedny et al. (2009) demonstrated similar recruitment of theory of mind networks in blind and sighted adults when reasoning about beliefs formed based on seeing and when reasoning about beliefs formed based on hearing. However, visual input does have some effect on theory of mind development, as congenitally blind children show delays in passing standard tests of mentalizing (Minter et al., 1998; Peterson et al., 2000; Green et al., 2004; Roch-Levecq, 2006), and some have even been described as having 'autistic-like' features including impairments in understanding and interacting with other people (Brown et al., 1997; Hobson et al., 1999; Hobson and Bishop,

2003). These findings indicate that visually observing the eye gaze, facial expressions, and body positioning of other people likely facilitates theory of mind development. While the absence of visual experiences during development does not affect the locations and functional profiles of the brain regions involved in theory of mind processes, more research is needed to determine if the detection of socially salient information, regardless of modality is reliant on the normal development of these regions, and to what extent visual input can facilitate or inhibit this process.

In the future, it would be advantageous to examine more precisely the relationship between eye movements and brain activity. For instance, it may be useful to include the time points of fixations landing in *people* and *things* AOIs as additional regressors in the fMRI analyses. This type of analysis may provide information regarding the nature of the association between superior temporal cortex activity and participants' fixations to socially salient scene regions, and perhaps identify which brain areas are linked to viewing particular scene regions during the non-social condition. In addition, future experiments would also benefit from the addition of a 'free-view' condition with no task instruction, which would serve to establish a baseline against which the fixation data for social and non-social conditions could be compared. Furthermore, a variety of functional connectivity analyses can be employed on fMRI data to explore the correlation between the activity in a designated region of the brain and the activity in the rest of the brain, the activity from ROI-to-ROI, and the activity from voxel-to-voxel. Correlations can be calculated both at a particular time point and at a temporal lag, the latter of which has the potential to indicate the causal direction of a functional connection, or in other words, can suggest whether activity in one region is best predicted by the past or future activity in another region. Such analyses would be useful for identifying regions that send and / or receive signals to the right STS and perhaps determine when and where social and non-social signals from the same scene diverge in the brain.

#### **5.2.4 Functional Implications for Individuals with Social Cognition Disorders and Suggestions for Future Studies**

The studies presented in the previous chapters have shown that healthy individuals view and process scenes differently depending on whether they are interpreted as social or non-social.

Data from Chapter 3 showed that social interpretations of complex scenes were associated with an increase in the number and duration of fixations directed towards people in a scene, particularly their heads, while fixations during non-social interpretations were shifted away from these areas and directed instead towards the inanimate objects in a scene. Brain activity acquired at the same time as the eye data (Chapter 4) illustrated that the right superior and middle temporal cortices were selectively activated when participants were focusing on and thinking about people during the social condition and a separate group of regions including the parahippocampus, fusiform, and inferior temporal gyrus were preferentially activated during the non-social condition. In combination, data from both studies suggest that fixating the heads and bodies of the people in a scene helps us infer the thoughts and intentions of others, and implies that the right superior and middle temporal cortices are involved in processing the meaning embedded in social scenes and interactions.

Importantly, the experiments presented in this dissertation on healthy individuals also provide the foundations for future studies that would include individuals with social cognition disorders such as schizophrenia and autism spectrum disorders (ASD). Such studies have the potential to help unveil why these individuals experience social processing deficits. As mentioned in Chapter 1 (Section 1.4.2) individuals with schizophrenia have a decreased quality of life compared to the general population (Ruggeri et al., 2005). Two important aspects of social cognition that are affected in schizophrenia are their ability to mentalize and to their ability to perceive emotion (Green et al., 2005; Couture et al., 2006). While both domains have been shown to play a role in predicting patient outcome (Couture et al., 2006; Fett et al., 2011), the ability to mentalize may be the more critical of the two, as it is more strongly correlated with community functioning and quality of life compared to emotion perception (Fett et al., 2011; Maat et al., 2012).

A recent behavioral study by Chambon and colleagues (2011) investigated schizophrenia patients' ability to interpret basic and complex video clips of actors interacting with an object in either a socially relevant or a non-socially relevant manner. The authors reported that individuals with schizophrenia were able to infer basic non-social intentions correctly (i.e. simple goal of a motor act), but had difficulties inferring intentions in the more complex non-social condition (i.e. goal of a sequence of motor acts) and in both the basic and complex social conditions (i.e. goals achieved during reciprocal interaction) (Chambon et al., 2011). In addition, the study was

designed to determine the amount that individuals with schizophrenia relied on either motor information available from body positions of the people in the videos or on their own prior knowledge and expectations about the mental states and attitudes of others. They found that during the complex non-social condition, patients relied heavily on their prior expectations about the mental states of others while disregarding motor evidence and this pattern of interaction predicted the severity of 'positive' symptoms. The opposite occurred when individuals with schizophrenia interpreted social videos. Patients relied more on the movement of the actor than on their prior knowledge about the beliefs of others and this pattern of interaction predicted the severity of 'negative' symptoms (Chambon et al., 2011). The results of this study suggest that the inability of individuals with schizophrenia to produce accurate inferences about other people's intentions stems from abnormalities in the mechanisms that integrate sensory information from body positioning and movement with prior beliefs about the mental states and attitudes of others (Chambon et al., 2011). However, why and where in the brain this disturbance occurs is not known.

Although the studies presented in this dissertation used static stimuli rather than videos, the fMRI activity observed in right superior temporal cortex during the social condition suggests that this region might be where new social knowledge, including that from body position and inferred movement kinematics, is incorporated with previously attained social knowledge in order to help us interpret social situations. This idea is supported by studies showing that while several regions are activated by viewing body actions, the STS specifically responds when viewing biologically plausible movements (Beauchamp et al., 2002; Giese and Poggio, 2003; Thompson et al., 2005; Peelen et al., 2006). Research investigating social cognitive processing in patients with schizophrenia have reported mixed results, with some showing hypoactivations in STS (Pinkham et al., 2008; Murphy et al., 2010) and others showing hyperactivations (Farrer et al., 2004). Future studies could use the experimental paradigm of Study 2 to establish if individuals with schizophrenia show the same activation as healthy participants in right superior and middle temporal cortices during social interpretations of complex scenes. If there are observable differences specific to describing the actions and intentions of the people in the images during the social condition, this would lend support to the claim that the difficulties these individuals have in understanding and inferring the thoughts and actions of others is related to the abnormal functioning of superior temporal cortex.



The study described above by Chambon et al. (2011) demonstrates some intriguing findings, however because they only monitored patients' behavior, there is still much that is left unknown regarding the source of this behavior. Moreover, their stimuli, did not include the actors' faces or full bodies, but rather showed only the actors' hands and a set of blocks on a table. By combining aspects of their study with those from the studies presented in this document, several experiments can be designed that have the potential to elucidate why patients rely differently on motor information and prior knowledge when observing social versus non-social scenes. One possibility would be to repeat the experiments carried out by Chambon et al. in the scanner while patients' eye movements are recorded. This would provide more information regarding the neural mechanisms associated with inferring intentions from dynamic interactions, both social and non-social, as well as potentially pinpoint more precisely whether their inferences are related to patients spending more time viewing the people or the blocks in the scenes. It may be that individuals with schizophrenia fixate less on the faces and bodies of others compared to healthy participants, making it difficult for them to accurately infer the mental states of others. This is supported by earlier studies that have repeatedly shown individuals with schizophrenia to have dysfunctions in eye tracking (Holzman et al., 1974; Shagass et al., 1976; Iacono et al., 1982; Sweeney et al., 1992). For instance, these individuals show significant impairments in their ability to use contextual cues from visual investigations in order to modify emotional intensity judgments or make mental state assessments (Monkul et al., 2007; Green et al., 2008).

It would also be advantageous for future studies to use an experimental paradigm similar to the one reported herein to determine if schizophrenia patients show abnormalities in eye movement or brain activity to social compared to non-social interpretations of complex images that contain clear views of people's heads and bodies. Experiments measuring both eye movements and brain activity are especially important given that individuals with schizophrenia display impairments in identifying expressions of emotion and in interpreting intentions, rendering them unable to explain and predict the behavior of others and leaves them isolated from the community (Habel et al., 2000; Penn et al., 2000; Edwards et al., 2001; Kohler et al., 2003; Pinkham et al., 2003). Future studies, should aim to determine if the impairments in inferring intentions are related to abnormal eye movement and / or brain activity patterns for social versus non-social complex stimuli as well as if and how these abnormalities correlate with

symptoms, social functioning, and quality of life. Together, the results of such studies could help identify potential therapeutic targets for diminishing the social dysfunction in schizophrenia.

Schizophrenia is not the only disorder associated with poor social functioning and impairments in mentalizing about the thoughts and intentions of other people. Individuals with ASD also display deficits in identifying social cues and attributing mental states to others (Klin, 2000) and have abnormal viewing patterns when looking at social stimuli (Klin et al., 2002; Pelphrey et al., 2002). However, much is still unknown regarding the origin of these impairments.

Previous research suggests that the social disability of individuals with ASD may be related to an inability to differentiate social and non-social information within a visual scene. For example, a study by Klin et al. (2002), found that when viewing movie clips of social interactions, individuals with ASD visually fixated on the eye region of faces less than healthy individuals. They also discovered that the social competence of their ASD participants was correlated with the percentage of time they spent fixating on the mouth regions and the percentage of time they spent fixating on the background objects, but in differing directions. Higher fixation times for mouths were correlated with higher levels of social competence and lower levels of social impairment, whereas higher fixation times for objects were correlated with lower levels of social adaptation and increased levels of social disability (Klin et al., 2002). These findings are consistent with the idea that focusing on objects reduces the salience of social stimuli and subsequently reduces the ability to comprehend social situations (Dawson et al., 1998; Klin et al., 2000).

The correlation between fixation time on objects and social competence is particularly intriguing, given that the study by Klin et al. (2002) deliberately chose clips that contained as few ‘nonessential’ objects and events as possible in order to keep participants focused on the social actions. This raises several interesting questions. For one, how would the fixation patterns or the correlation between fixation patterns and social competence change when individuals with ASD view scenes containing more objects as well as a social situation? Moreover, what regions of the brain are active when individuals with ASD view social versus non-social information within a complex scene? The experimental design used in Studies 1 and 2, if repeated with the addition of ASD participants and a free-view condition, can be employed to help establish how individuals with ASD naturally view and process a complex scene, as well as determine if

instructing them to interpret the scenes based on social or non-social features alters their eye movement patterns and brain activity to those scenes.

The results of previous neuroimaging studies imply that individuals with ASD have improper functioning of the brain regions usually responsible for processing social information, and instead show activation in a variety of other regions. For instance, compared to healthy participants, individuals with ASD show increased activity in lateral temporal cortex when performing a face discrimination task, a region that is usually associated with object processing (Schultz et al., 2000). In another study investigating brain activity during a face perception task (compared to a shape perception control), individuals with ASD demonstrated reaction times and accuracy measures that were not significantly different from healthy participants; however, their brain activity patterns while performing the task were significantly different (Pierce et al., 2001). While activation was observed in similar regions of fusiform gyrus, amygdala, and STS for all healthy participants, none of these typical face-processing regions was significantly active in ASD participants. Rather, only ‘deactivations’ or ‘reverse-activations’ in postcentral gyrus, inferior parietal lobe, cingulate, and parahippocampal gyrus were observed at the group level in ASD participants. Exploring the data at the single participant level revealed that face processing was associated with a unique set of activated regions for every ASD participant (e.g. frontal cortex, primary visual cortex, and cerebellum). The results of this study suggest that although individuals with ASD were able to identify a female face and a circle with similar speed and accuracy as healthy participants, different neural mechanisms are working to accomplish these tasks in healthy individuals compared to individuals with ASD. The authors additionally propose that the regions of deactivation consistently observed in ASD participants reflect enhanced processing of the shape-perception control task compared to the face perception task (Pierce et al., 2001). Together, these studies support the idea that individuals with ASD are not equipped with the same specialized mechanisms for processing social stimuli as healthy individuals, but during certain basic social tasks, their brain may be able to compensate by rerouting this information to other regions such as those for object processing. Such compensatory mechanisms would likely not be enough to support the processing of complex social tasks such as those involving mentalizing about the thoughts and intentions of others.

Dysfunction of the STS, in particular the right STS, in ASD has been revealed across several types of tasks. For instance, while healthy individuals exhibit activity in the right

posterior STS that is sensitive to the congruency between a given biological motion (e.g. reaching towards a cup) and a prior emotional context (e.g. smiling), individuals with ASD do not show differential activity in posterior STS as a function of congruency (Wyk et al., 2009; Pelphrey et al., 2011). Other neuroimaging studies have shown STS dysfunction in ASD during tasks of eye movement perception (Pelphrey et al., 2005), the attribution of intentions (Castelli et al., 2002), and human speech perception (Boddaert et al., 2003; Gervais et al., 2004). Although the exact cause of the STS abnormalities in ASD is not yet known, potential factors include hypoperfusion in bilateral temporal lobe areas (Ohnishi et al., 2000; Zilbovicius et al., 2000) and gray matter density abnormalities in STS (Boddaert et al., 2004), both of which have been identified in children with ASD.

Research on the developing brain and genetics are providing some interesting insights into the mechanisms of human social processing that might underlie the social abnormalities present in ASD. For instance, a study by Nelson et al. (2001) reported elevated concentrations of brain growth factors in ASD neonates compared to children with cerebral palsy and healthy children. This finding suggests that the brains of ASD individuals may not be optimally organized for environmental stimulation even at early age, and thus perpetuate further abnormalities not only within the brain, but also in the social abilities of these individuals (Nelson et al., 2001). Investigations into the genetics of social processing in healthy individuals have demonstrated that the cannabinoid receptor 1 gene is associated with a greater striatal response to happy faces compared to disgust faces and this increased striatal response to happy faces was also associated with longer gaze durations to happy faces (Chakrabarti et al., 2006; Chakrabarti and Baron-Cohen, 2011). These data imply that the ability to perceive and process signals of social reward is established at the genetic level, with the cannabinoid receptor 1 gene being linked to both eye movement and brain activity to positive social and emotional stimuli.

Based on these findings, it is not surprising that the cannabinoid receptor 1 gene appears to have a role in a variety of social disorders. Individuals with depression and anxiety carrying certain alleles of this gene display treatment resistance and hypo-responsiveness to social reward stimuli in subcortical brain regions (Domschke et al., 2008). In addition, reduced expression of the cannabinoid receptor 1 gene has been identified in postmortem brain tissue of individuals with ASD (Purcell et al., 2001). Collectively, these studies suggest that the social impairments present in ASD may result from reduced expression of the cannabinoid receptor 1 gene that in

turn may lead to a reduced response to social rewards such as happy faces, thus making social interactions less reinforcing and further worsening their social difficulties (Dawson et al., 2002; Chakrabarti and Baron-Cohen, 2011). The cannabinoid receptor 1 gene however, is only one of several other potential candidate genes speculated to regulate complex traits related to social functioning (Ebstein et al., 2010). There is still much to be learned regarding the nature of social impairments in ASD. Future studies should aim to combine methodologies to gain a more comprehensive understanding of the disorder. For instance, the experimental paradigm and methods presented in Chapters 3 and 4 could be combined with genotyping to determine if the cannabinoid receptor 1 gene is related to eye movement and brain activity (in non-striatal regions) to visual images of complex social scenes and could be further extended to include individuals with ASD or even schizophrenia.

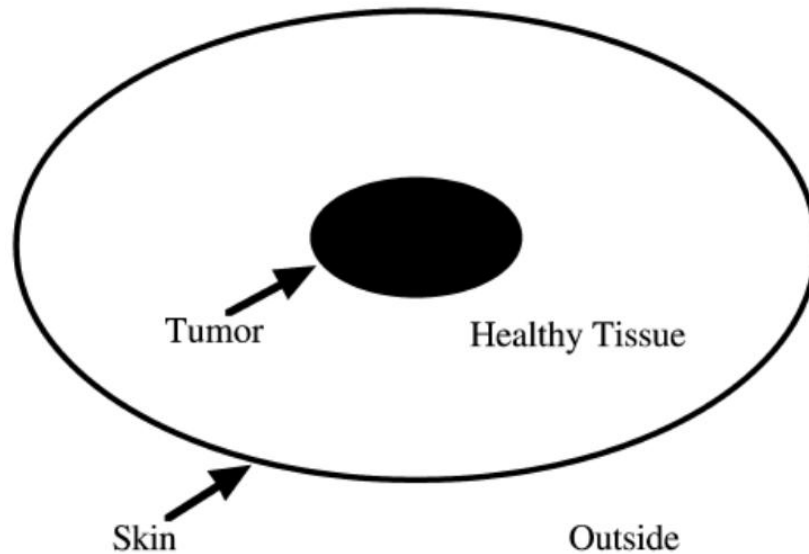
Taken together, the abnormal visual search abilities and improper integration of social information in individuals with social cognition disorders demonstrate the multi-layered nature of social cognition impairments and highlight the need for further investigation into the relationships between viewing social scenes and the neural responses to those scenes in both healthy and impaired individuals. Emerging research indicates that with training, individuals with ASD and schizophrenia may be able to ameliorate some of their social deficits. For instance, several studies have demonstrated that after facial affect training, individuals with schizophrenia are significantly improved in facial affect recognition, with recognition performance after training approaching the level of healthy individuals (Frommann et al., 2003; Wölwer et al., 2005; Kayser et al., 2006). Similarly, individuals with ASD are able to not only increase their behavioral sensitivity to faces, but also improve their neural response efficiency to faces and emotional expressions after training (Silver and Oakes, 2001; Bölte et al., 2002; Bölte et al., 2006; Golan and Baron-Cohen, 2006; Golan et al., 2010; Tanaka et al., 2010; Faja et al., 2012). Individuals with social cognition disorders additionally show social skill improvements after training with more complex social-emotional stimuli such as pictures and videos that depict objects or social interactions. These types of stimuli are proving to be effective tools for helping people with social cognition disorders increase their social communicative behaviors and develop their theory of mind skills (e.g. Bondy and Frost, 2001; Charlop-Christy et al., 2002; Kayser et al., 2006; Horan et al., 2011). In the future, the manipulated TAT images presented herein could be utilized as stimuli for social skills training and included as part of a therapeutic

intervention for social cognition disorders, especially given their complexity and social relevancy, which makes them ideal for targeting mental state attribution abilities.

### 5.3 Conclusions

In conclusion, the proper execution of adaptive behavior depends on attentional selectivity - the ability to highlight, process, and act on only some elements of a stimulus array while simultaneously ignoring and discarding others (Holland and Gallagher, 1999). The data presented in this dissertation demonstrate that interpreting identical scenes based on socially relevant components or non-social inanimate objects leads to distinct patterns of eye movement and brain activation. Each gaze pattern and network of brain regions was consistent with attending to and processing only one category of information (people OR things), despite both categories being present in all images. This type of design, in part, resembles how we experience social interactions in the real world, with the people, background objects, and context remaining present, while our locus of attention within that environment may vary. Furthermore, this work provides evidence that the use of separate stimuli to investigate different categories of information is not always necessary. By using images that are more naturalistic and intrinsically complex, and methodically altering how these images are viewed or interpreted, a better understanding for how we approach and process social information can be obtained in a more realistic way. Studying the eye movement and underlying neural activity associated with processing complex social information in healthy individuals is a critical first step towards understanding the impairments present in individuals with social cognition disorders.

## 5.4 Figures



**Figure 5-1.** A diagram depicting Duncker's radiation problem (Duncker, 1945). Eye tracking studies by Grant and Spivey (2003) and Thomas and Lleras (2007) instructed participants to view the diagram and determine how to destroy the tumor without damaging the healthy tissue surrounding it. The correct solution entailed firing several weak-intensity lasers from outside the tumor, which together would have enough intensity to destroy the tumor, but not the healthy tissue. The labels indicating diagram features were not visible during the experiment, but were verbally explained to participants prior to the experiment. Figure and caption adapted from other sources (Duncker, 1945; Grant and Spivey, 2003; Thomas and Lleras, 2007).



## **APPENDIX**

## **A.1 Forms**

The following two forms were given to all participants to fill out before participation in experiments. The first form (Edinburgh Handedness) was used to determine participants' handedness (right- or left-handed), while the second form (MRI Examination Information and Education Form), identified potential reasons for exclusion from participating in the fMRI experiment. Any participant who reported being pregnant, having metal or unsafe bodily implants, or were taking psychotropic medications (e.g. for depression) were disqualified from the study. These forms contained information of a personal and sensitive nature and were therefore locked in a filing cabinet once completed.



## Center for Advanced Imaging, West Virginia University

### Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities by putting a check in the appropriate column. If a preference is so strong that you would never try to use the other hand, unless absolutely forced to, put 2 checks. If in any case you are really indifferent put a check in both left and right columns.

Some of the activities listed below require the use of both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try and answer all of the questions, and only leave a blank if you have no experience at all with the object or task.

| ACTIVITY                                    | LEFT  | RIGHT   |
|---|---|---|
| 1. Writing                                  | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 2. Drawing                                  | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 3. Throwing                                 | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 4. Scissors                                 | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 5. Toothbrush                               | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 6. Knife (without fork)                     | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 7. Spoon                                    | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 8. Broom (upper hand)                       | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 9. Striking Match (match)                   | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| 10. Opening box (lid)                       | <input type="checkbox"/> <input type="checkbox"/> | <input type="checkbox"/> <input type="checkbox"/> |
| <b><u>TOTAL</u></b><br>(X's in each column) | <input type="text"/>                              | <input type="text"/>                              |

Percent Handedness Score = (Total Right – Total Left) X 5 = \_\_\_\_\_

# CENTER FOR ADVANCED IMAGING

## MRI EXAMINATION INFORMATION AND EDUCATION FORM



TO BE COMPLETED BY THE PARTICIPANT

**ATTENTION:** *It is important that you complete this form entirely*

Do you have a history of diabetes?

☐ Yes

☐ No

Do you have a history of kidney disease?

☐ Yes

☐ No

List all surgeries with dates, if known:

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List all current medication:

---

---

Please list all allergies:

---

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### PLEASE CHECK ALL THAT APPLY:

- |  |   |   |
|--|---|---|
| <input type="checkbox"/> head surgery                  | <input type="checkbox"/> insulin/infusion pumps | <input type="checkbox"/> heart surgery          |
| <input type="checkbox"/> brain surgery                 | <input type="checkbox"/> body piercings         | <input type="checkbox"/> PICC line              |
| <input type="checkbox"/> aneurysm clips                | <input type="checkbox"/> pacemaker              | <input type="checkbox"/> bladder implant        |
| <input type="checkbox"/> eye implants                  | <input type="checkbox"/> port                   | <input type="checkbox"/> Vagus nerve stimulator |
| <input type="checkbox"/> eye surgery                   | <input type="checkbox"/> back surgery           | <input type="checkbox"/> colored contact lenses |
| <input type="checkbox"/> ear implants (cochlea/stapes) | <input type="checkbox"/> surgical clips         |   |
| <input type="checkbox"/> metal in eyes (eye weights)   | <input type="checkbox"/> surgical rods          |   |
| <input type="checkbox"/> welding, grinding, metal work | <input type="checkbox"/> surgical pins          |   |
| <input type="checkbox"/> shrapnel                      | <input type="checkbox"/> joint replacement      |   |
| <input type="checkbox"/> pregnant                      | <input type="checkbox"/> shunts                 |   |
| <input type="checkbox"/> breast feeding                | <input type="checkbox"/> stents                 |   |
| <input type="checkbox"/> claustrophobic                | <input type="checkbox"/> Vena Cava filter       |   |
| <input type="checkbox"/> penile implants               | <input type="checkbox"/> aortic clips           |   |
| <input type="checkbox"/> IUD                           | <input type="checkbox"/> heart valves           |   |
| <input type="checkbox"/> tattoos                       | <input type="checkbox"/> history of cancer      |   |

Other (please specify):

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Any other information that you feel may be pertinent to your study, please list below:

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The above information is complete and correct. This sheet has been fully explained to me and I have had the opportunity to express all concerns and questions about my exam.

---

Participant Signature

---

Date

## A.2 Stimuli

The following 12 drawings served as stimuli in all of the experimental studies presented here, and are a subset of the images making up the Thematic Apperception Test (TAT) series (Murray, 1943). The images from the TAT were the ideal choice of stimuli because they are behaviorally validated and because they portray a range of compelling social and interpersonal situations that would promote active visual investigations and cognitive processes.

The TAT is a projective personality test consisting of 31 images of somewhat ambiguous yet provocative nature that were created with the intention of gauging participants' underlying patterns of thought, attitudes, interests, observational capacity, and emotions. In the original administration procedure, only certain images were presented depending on the age and gender of the participant and were labeled as such. The numbers listed above each picture on the following pages therefore not only indicate the number of the image in the series, but also the category of participant to which they were to be administered, including men (M), women (F), boys (B), and girls (G). If no letter qualifiers are present, this meant they were suitable for use with all participants. In our studies however, the descriptors were simply used as a way to reference the image, and all images were shown to all participants regardless of their gender.

Since the main objective of our experiments was to investigate social versus non-social processes, we selected the following 12 drawings: 1, 2, 4, 5, 6BM, 6GF, 7GF, 8BM, 9GF, 12M, 13MF, 15. These specific images were chosen based on their depiction of a person or persons (with clearly seen full or 3/4 facial views) involved in a potentially challenging situation or social interaction set amongst a variety of background objects. Note that the final stimulus images used in our experiments are modified versions of the original TAT pictures, created by centering each drawing on a grey background and then overlaying it with a grid of 13 crosshairs.

1



2



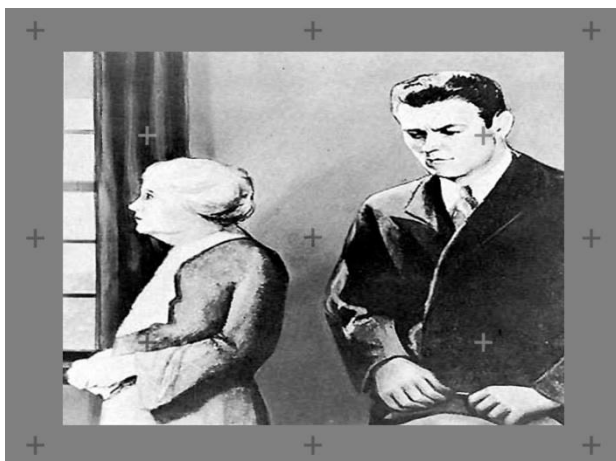
4



5



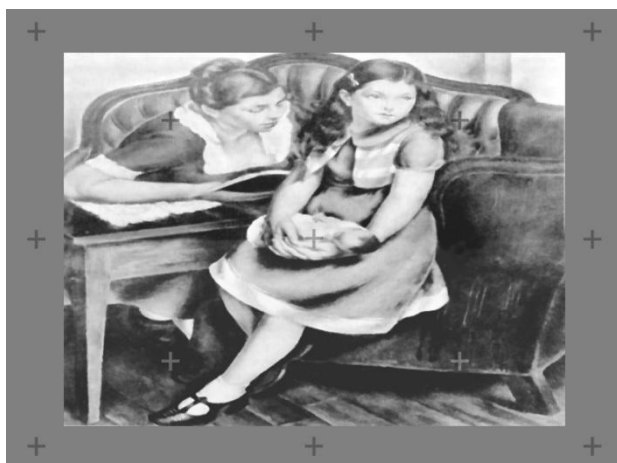
6BM



6GF



**7GF**



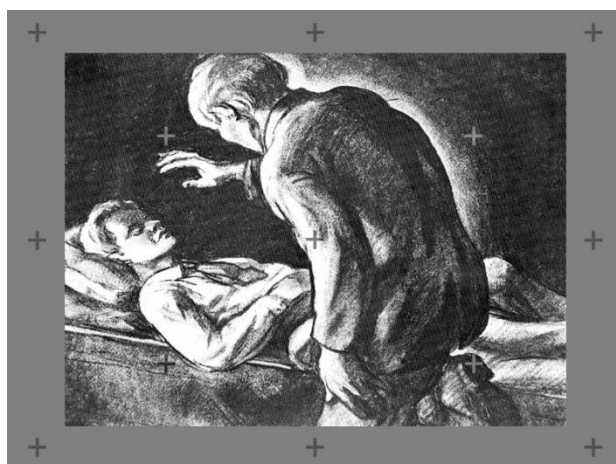
**8BM**



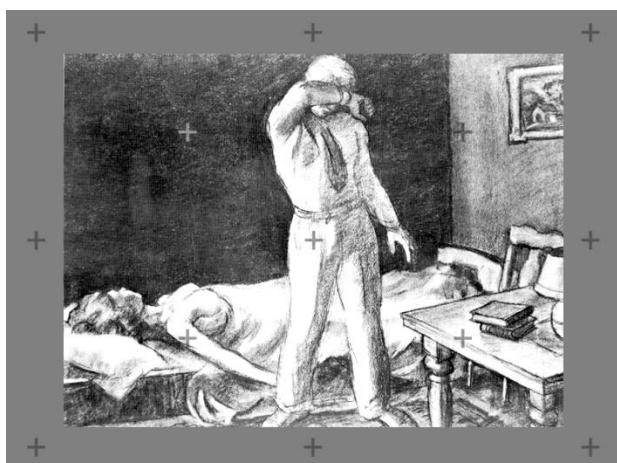
**9GF**



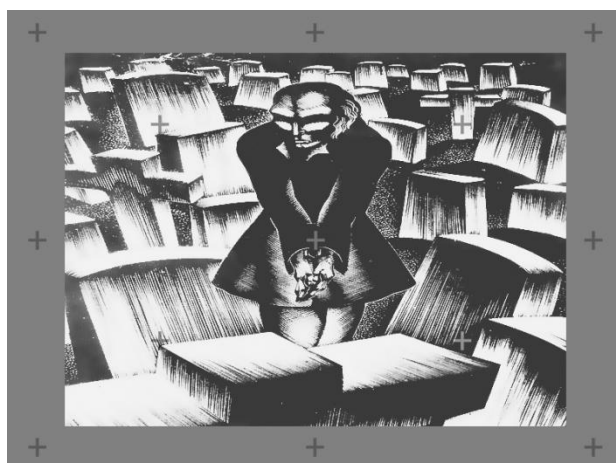
**12M**



**13MF**



**15**





## A.3 Additional Eye Movement Data Analyses

The next sections describe various steps in the eye movement data analysis procedure that were carried out, but have not been discussed in detail elsewhere in this dissertation. First, a brief overview of the criteria used when drawing areas of interest (AOIs) on stimulus images is presented. Next, the results of the analysis on the original data for all three conditions is recounted and discussed. This is followed by an explanation of why and how participants' eye movement data was normalized for AOI pixel area. Lastly, the results of the normalization analysis on fixation number and duration data are presented and briefly discussed.

### A.3.1 AOIs

Prior to eye data analysis, AOIs were drawn closely around each person, object, and crosshair on all stimulus images and these formed the three AOI groups: *people*, *things*, and *crosshairs*. It was important to outline all AOIs in a consistent manner; however, the 13 crosshairs on each image were usually much smaller than the people or objects present in the scenes. Although the *people* and *things* AOIs were drawn closely following the edges of each person or object, if the crosshairs outlines followed this exact method, they would likely be too small and any fixations occurring in them would not be registered by the eye tracker. On the other hand, to maintain outline consistency with the other AOI groups, the crosshairs AOIs could not extend too far beyond their borders. Thus, a box was drawn around each crosshair whose size we thought maintained the best balance between size and similarity to the other AOI outlines. It is important to note that AOIs did overlap, for instance, an object AOI (e.g. bracelet) would be located partially or completely within a person AOI. Overlap in major areas (e.g. heads) was avoided where possible, but some overlap was inevitable due to the complexity of the images. Figure A.3-1 depicts single examples of the AOIs drawn for each of the three categories.

### A.3.2 General Statistical Methods

Both the original data and the normalized data were analyzed using the same statistical methods. Participant's data for fixation number and duration were analyzed in IBM SPSS

Statistics (Release 19.0.0, SPSS Inc.) using the General Linear Model and within-subjects factors of Condition (People, Things, Crosshairs) and AOI (*people*, *things*, *crosshairs*). Significance was determined by  $p < 0.05$  (Greenhouse-Geisser corrected). Relevant pairwise comparisons ( $p < 0.05$ , Bonferroni corrected for multiple comparisons) were performed.

### A.3.3 Original Eye Movement Data: Results

Number of fixations as a function of interpretation condition. Initial qualitative visual inspection of participants' eye gaze paths indicated unique patterns of fixations for the three conditions (People and Things displayed in Chapter 3, Section 3.6, Figure 3-3; Crosshairs shown below in Figure A.3-2A). Using the General Linear Model on the total number of fixations made by participants and within-subjects factors of Condition (People, Things, Crosshairs) and AOI (*people*, *things*, *crosshairs*) we found a significant main effect of Condition ( $F[2,16] = 7.74$ ,  $p = 0.009$ ). Contrasts indicated that this effect was due to significantly fewer fixations when participants were cued to focus on the grid of crosshairs (Crosshairs condition) compared to when cued to describe the thoughts and actions of people (People condition;  $F[1,8] = 10.67$ ,  $p = 0.011$ ) and when cued to focus on the functions and properties of objects in the scene (Things condition;  $F[1,8] = 18.76$ ,  $p = 0.003$ ). There was no significant difference in fixation number between People and Things conditions ( $F[1,8] = 0.434$ ,  $p = 0.529$ ). There was a significant main effect of AOI ( $F[2,16] = 65.15$ ,  $p < 0.001$ ), with contrasts revealing significantly fewer fixations to *crosshairs* AOIs in the images relative to *people* ( $F[1,8] = 64.81$ ,  $p < 0.001$ ) and *things* AOIs ( $F[1,8] = 150.87$ ,  $p < 0.001$ ). Again, no significant differences were observed between the number of fixations occurring in *people* and *things* AOIs ( $F[1,8] = 3.98$ ,  $p = 0.081$ ). Means and standard errors for the number of fixations as a function of Condition and AOI are listed in Table A.3-1 and displayed graphically in Figure A.3-2B (colored bars indicate Condition; patterned rectangles indicate AOI category)

Interestingly, although there was no statistical difference between the People and Things conditions, or *people* and *things* AOIs with respect to the number of total fixations, there was a significant interaction effect between Condition and AOI ( $F[4,32] = 23.59$ ,  $p < 0.001$ ). This interaction was explored with pairwise comparisons using a Bonferroni correction. When investigating the distribution of fixation numbers within each condition, analyses indicated that

during the People condition, participants made significantly more fixations in *people* AOIs relative to both *things* ( $p = 0.006$ ) and *crosshairs* ( $p < 0.001$ ) AOIs (Figure A.3-2B, patterned rectangles in green bar), with *things* AOIs also having significantly more fixations than *crosshairs* AOIs ( $p < 0.001$ ). For the Things condition, the number of fixations occurring in *things* AOIs tended to be higher than the number in *people* AOIs, with the results trending to statistical significance ( $p = 0.055$ ; Figure A.3-2B, patterned rectangles in blue bar). There were, however, significantly more fixations in *things* ( $p < 0.001$ ) and *people* ( $p < 0.001$ ) AOIs than in *crosshairs*. Lastly, for the Crosshairs condition, the number of fixations made in *people* and *things* AOIs were not significantly different, but the number of fixations in both of these AOI categories was significantly higher than the number for *crosshairs* AOIs (*people*,  $p < 0.001$ ; *things*,  $p < 0.001$ ; Figure A.3-2B, patterned rectangles in pink bar).

When examining the number of fixations in each AOI category across conditions, the number of fixations landing in *people* AOIs was greatest for the People condition relative to the Things ( $p = 0.011$ ) and Crosshairs ( $p = 0.005$ ) conditions, with no difference in the mean number of fixations made in *people* AOIs between the Things and Crosshairs conditions (Figure A.3-2B, bottom patterned rectangle in all colored bars). The number of fixations directed to *things* AOIs was highest during the Things condition compared to People ( $p = 0.004$ ) and Crosshairs ( $p < 0.001$ ) conditions, with no difference in the number of fixations to *things* between People and Crosshairs conditions (Figure A.3-2B, middle patterned rectangle in all colored bars). The *crosshairs* AOIs were fixated a similar number of times across all conditions (Figure A.3-2B, top patterned rectangle in all colored bars).

Total time spent fixating the images as a function of interpretation condition. Differences in the total time spent fixating the images were also examined using the General Linear Model and within-subjects factors of Condition (People, Things, Crosshairs) and AOI (*people*, *things*, *crosshairs*). This analysis returned a significant main effect of Condition ( $F[2,16] = 18.57$ ,  $p = 0.002$ ). Contrasts demonstrated that there were longer fixation durations for the People ( $F[1,8] = 21.21$ ,  $p = 0.002$ ) and Things ( $F[1,8] = 171.56$ ,  $p < 0.001$ ) conditions than for Crosshairs, while durations for People were not significantly different from Things ( $F[1,8] = 1.492$ ,  $p < 0.001$ ). There was also a significant main effect of AOI ( $F[2,16] = 59.22$ ,  $p = 0.257$ ). Contrasts revealed that overall, *people* ( $F[1,8] = 58.07$ ,  $p < 0.001$ ) and *things* ( $F[1,8] = 197.09$ ,  $p < 0.001$ ) AOIs were fixated longer than *crosshairs*, but fixation durations for *people* and *things* AOIs were not

significantly different from one another ( $F[1,8] = 2.54, p = 0.15$ ). Means and standard errors for fixation duration as a function of Condition and AOI are listed in Table A.3-1 and displayed graphically in Figure A.3-2C.

As with the results for fixation number, there was also a significant Condition by AOI interaction effect for the duration of fixations ( $F[4,32] = 22.41, p < 0.001$ ). Pairwise comparisons identified that in the People condition, participants fixated *people* AOIs significantly longer than both *things* ( $p = 0.01$ ) and *crosshairs* ( $p < 0.001$ ) AOIs, with *things* AOIs also being fixated more than *crosshairs* AOIs ( $p < 0.001$ ; Figure A.3-2C, patterned rectangles in green bar). For the Things condition, significantly longer fixations occurred in *things* AOIs ( $p < 0.001$ ) and *people* AOIs ( $p < 0.001$ ) relative to *crosshairs* (Figure A.3-2C, patterned rectangles in blue bar). Fixation durations in *things* AOIs tended to be longer than those in *people*, but this difference was not significant ( $p = 0.092$ ). The fixation durations within the Crosshairs condition parallel the results for fixation number, in that durations were not significantly different between *people* and *things* AOIs, but both of these AOIs were viewed significantly longer than *crosshairs* AOIs (*people*,  $p < 0.001$ ; *things*,  $p < 0.001$ ; Figure A.3-2C, patterned rectangles in pink bar).

Finally, the fixation duration data as measured from an AOI across Condition perspective show that fixations in *people* AOIs were longest during the People condition relative to the Things ( $p = 0.006$ ) and Crosshairs ( $p = 0.002$ ) conditions, with mean durations in *people* AOIs between Things and Crosshairs not being significantly different (Figure A.3-2C, bottom patterned rectangle in all colored bars). Fixations within *things* AOIs were longest during the Things condition compared to People ( $p = 0.003$ ) and Crosshairs ( $p < 0.001$ ), while mean durations in *things* AOIs during the People and Crosshairs conditions were not significantly different (Figure A.3-2C, middle patterned rectangle in all colored bars). Durations for *crosshairs* AOIs were slightly longer in the Crosshairs condition compared to People and Things, but this difference was not significant. The amount of time spent fixating *crosshairs* AOIs between the People and Things conditions was also not significant (Figure A.3-2C, top patterned rectangle in all colored bars).

#### A.3.4 Original Eye Movement Data: Discussion

Eye movement data for the three conditions showed that although there was no difference in fixation number or duration across the social and non-social domains at the level of the whole scene (i.e. when effects of Condition *or* AOI are considered independently), the interaction effect indicated that the location of fixations was significantly affected by interpretation condition. For instance, during the People condition participants focused longer and more frequently on the protagonists of the scene at the expense of objects, whereas the reverse tended to be true during the Things condition.

Results from the Crosshairs condition were unlike the other conditions, in that the largest proportion of fixations did not fall within the *crosshairs* AOIs, as one would expect. Additionally, *crosshairs* AOIs were fixated similarly across all three conditions. Several methodological factors might have facilitated these observed fixation patterns in the Crosshairs condition and *crosshairs* AOIs: AOI positioning within the images, task instruction during the Crosshairs condition, and the amount of pixel area covered by each AOI category. As mentioned above, great effort was made to position *crosshairs* AOIs so that they would not interfere with salient visual features; however, some overlap of *crosshairs* AOIs with those from the other categories was unavoidable. Other reasons for overlapping AOIs were the result of trying to keep crosshair locations similar to those in the calibration grid for the eye tracker, and to prevent crosshair positions from varying across images. Consequently, the eye tracking software may not have been able to delineate between fixations occurring within a *crosshairs* AOI relative to another immediately adjacent (non-crosshairs) AOI given its spatial resolution. The observed equivalent increase in the number of fixations counted in *people* and *things* AOIs during the Crosshairs condition might reflect such a process.

A second factor for the observed decrease in fixations during the Crosshairs condition could be that participants were not instructed to view the crosshairs (or people or things) at any particular speed or to fixate on them for a given duration. The short fixations we observed suggest that participants made quick saccades from crosshair to crosshair in the images without fully stopping on each one. This may have precluded the detection of fixations during this condition since the analysis software for the eye tracker was set to count fixations only if they were above 80 ms in length.

A third possibility was that the observed patterns of fixations across Conditions and AOIs were not due to differences in attentional saliency, but were instead related to inequalities in the amount of surface area covered by each AOI category. To rule this out, we normalized the data for pixel area and then reanalyzed the data using the same statistical analyses methods. The procedure for normalizing participants' eye data and the subsequent analysis and results of this normalization are described and discussed in the next sections.

### **A.3.5 Normalization for AOI Pixel Area: Analysis Procedures**

It was possible that the method used when drawing AOIs may have led to inequalities in the amount of surface area covered by each AOI category. To rule this out, we normalized the eye movement data (fixation number and duration) for AOI pixel area. This was accomplished by using Adobe Photoshop CS3 (version 10.0.1; Adobe Systems, Inc) to measure the total number of pixels in each picture as well as the number of pixels in each of the AOIs for all images. The number of pixels for each AOI category was summed for each individual stimulus image. Then the proportion of pixels held by the three AOI categories per image was calculated by dividing the combined total number of pixels for each AOI category by the overall total number of pixels in the image. The next step was to calculate the ratio of *crosshairs* AOI pixel area to *people* and *things* AOI pixel area for each image and use these unique numbers to adjust participants' eye movement data. Table A.3-2 below lists the total overall pixels, the combined number of pixels in each AOI group, the proportion of total pixels held by each AOI category, and the calculated ratio of *crosshairs* AOI pixels to *people* and *things* AOIs for all stimulus images used in the experiment.

### **A.3.6 Normalization for AOI Pixel Area: Results**

Number of fixations as a function of interpretation condition. The General Linear Model was applied on the total number of fixations made by participants and within-subjects factors of Condition (People, Things, Crosshairs) and AOI (*people*, *things*, *crosshairs*). We found a significant main effect of Condition ( $F[2,16] = 6.35, p = 0.02$ ), and contrasts indicated that this effect was due to significantly fewer fixations during the Crosshairs condition compared to the People condition ( $F[1,8] = 10.42, p = 0.012$ ) and the Things condition ( $F[1,8] = 11.15, p = 0.01$ ).

There was no significant difference in fixation number between People and Things conditions ( $F[1,8] = 1.56, p = 0.247$ ). There was a significant main effect of AOI ( $F[2,16] = 31.03, p < 0.001$ ), with contrasts revealing significantly fewer fixations overall regardless of condition to *crosshairs* AOIs relative to *people* ( $F[1,8] = 39.12, p < 0.001$ ) and *things* AOIs ( $F[1,8] = 20.77, p = 0.002$ ). Contrasts showed that overall there were significantly more fixations in *people* AOIs compared to *things* AOIs ( $F[1,8] = 23.58, p = 0.001$ ). Means and standard errors for the normalized number of fixations as a function of Condition and AOI are listed in Table A.3-3, with the means being displayed graphically in Figure A.3-3A (colored bars indicate Condition; patterned rectangles indicate AOI category).

Although there was no statistical difference between the People and Things conditions with respect to the number of total fixations, there was a significant interaction effect between Condition and AOI ( $F[4,32] = 16.35, p < 0.001$ ). This interaction was explored with pairwise comparisons using a Bonferroni correction. During the People condition, participants made significantly more fixations in *people* AOIs relative to both *things* ( $p = 0.003$ ) and *crosshairs* AOIs ( $p = 0.002$ ; Figure A.3-3A, patterned rectangles in green bar). There was no significant difference between the number of fixations directed to *things* AOIs and *crosshairs* AOIs during the People condition. For the Things condition, the number of fixations occurring in *things* AOIs was not significantly different from those to *people* AOIs (Figure Figure A.3-3A, patterned rectangles in blue bar). There were, however, significantly more fixations in both *things* AOIs ( $p = 0.008$ ) and *people* AOIs ( $p = 0.001$ ) than in *crosshairs* AOIs. Lastly, for the Crosshairs condition, the number of fixations made in *people* AOIs was significantly higher than those made to *things* AOIs ( $p = 0.021$ ) and *crosshairs* AOIs ( $p = 0.006$ ), but the number of fixations in *things* AOIs was not significantly different from *crosshairs* AOIs (Figure A.3-3A, patterned rectangles in pink bar).

Examining the number of fixations in each AOI category across conditions showed that the number of fixations landing in *people* AOIs was greatest for the People condition relative to the Things ( $p = 0.034$ ) and Crosshairs ( $p = 0.005$ ) conditions. There was no difference in the mean number of fixations made in *people* AOIs between the Things and Crosshairs conditions (Figure A.3-3A, bottom patterned rectangle in all colored bars). The number of fixations directed to *things* AOIs was highest during the Things condition compared to People ( $p = 0.003$ ) and Crosshairs ( $p < 0.001$ ) conditions, with no difference in the number of fixations to *things*

between People and Crosshairs conditions (Figure A.3-3A, middle patterned rectangle in all colored bars). The *crosshairs* AOIs were fixated a similar number of times across all conditions (Figure A.3-3A, top patterned rectangle in all colored bars).

Total time spent fixating the images as a function of interpretation condition. Differences in the total time spent fixating the images was again examined using the General Linear Model and within-subjects factors of Condition (People, Things, Crosshairs) and AOI (*people*, *things*, *crosshairs*). This analysis returned a significant main effect of Condition ( $F[2,16] = 12.98, p = 0.005$ ). Contrasts demonstrated that there were longer fixation durations for the People ( $F[1,8] = 18.99, p = 0.002$ ) and Things ( $F[1,8] = 57.33, p < 0.001$ ) conditions than for Crosshairs, while durations for People were not significantly different from Things ( $F[1,8] = 3.96, p = 0.082$ ). There was also a significant main effect of AOI ( $F[2,16] = 24.74, p < 0.001$ ). Contrasts revealed that overall, *people* ( $F[1,8] = 31.33, p = 0.001$ ) and *things* ( $F[1,8] = 26.80, p = 0.001$ ) AOIs were fixated longer than *crosshairs* AOIs, and *people* AOI fixation durations were significantly longer than *things* AOIs ( $F[1,8] = 16.94, p = 0.003$ ). Means and standard errors for pixel normalized fixation durations as a function of Condition and AOI are listed in Table A.3-3, with the means being displayed graphically in Figure A.3-3B (colored bars indicate Condition; patterned rectangles indicate AOI category).

As with the results for fixation number, there was also a significant Condition by AOI interaction effect for the duration of fixations ( $F[4,32] = 15.46, p = 0.001$ ). Pairwise comparisons identified that in the People condition, participants fixated *people* AOIs significantly longer than both *things* ( $p = 0.005$ ) and *crosshairs* ( $p = 0.003$ ) AOIs, with *things* AOIs also being fixated significantly longer than *crosshairs* AOIs ( $p = 0.017$ ; Figure A.3-3B, patterned rectangles in green bar). For the Things condition, significantly longer fixations occurred in *things* AOIs relative to *crosshairs* AOIs ( $p = 0.003$ ) and in *people* AOIs compared to *crosshairs* AOIs ( $p = 0.001$ ), but fixation durations in *things* AOIs were not significantly different from fixation durations in *people* AOIs (Figure A.3-3B, patterned rectangles in blue bar). The fixation durations within the Crosshairs condition were not significantly different between any of the AOI categories (Figure A.3-3B, patterned rectangles in pink bar).

Finally, the fixation duration data as measured from an AOI across Condition perspective show that fixations in *people* AOIs were longest during the People condition relative to the Things ( $p = 0.024$ ) and Crosshairs ( $p = 0.003$ ) conditions. Mean durations in *people* AOIs during



the Things condition were also longer than in the Crosshairs condition ( $p = 0.015$ ; Figure A.3-3B, bottom patterned rectangle in all colored bars). Fixations within *things* AOIs were longest during the Things condition compared to People ( $p = 0.004$ ) and Crosshairs ( $p = 0.001$ ), while mean durations in *things* AOIs during the People and Crosshairs conditions were not significantly different (Figure A.3-3B, middle patterned rectangle in all colored bars). Durations for *crosshairs* AOIs were slightly longer in the Crosshairs condition compared to the People and Things conditions, but this difference was not significant, nor was the fixation time in *crosshairs* AOIs between People and Things conditions (Figure A.3-3B, top patterned rectangle in all colored bars).

### A.3.7 Normalization for AOI Pixel Area: Discussion and Comparison to Original Data

Normalizing participants' eye movement data was performed to help characterize the data and eliminate any effects that might be due to unequal pixel areas covered by the three AOI categories. More specifically, we wanted to determine if the low number and duration of fixations observed to crosshairs AOIs, especially during the Crosshairs condition, were related to their smaller size compared to the other AOI groups. After adjusting participant data for AOI area, we repeated the same statistical analysis methods in SPSS that were used on the original data.

In general, it was determined that analysis of the normalized fixation number and duration data produced results that were relatively equivalent to the original data, although there were a few differences. The main difference was the mean number and duration of fixations in the *things* and *people* AOIs observed during the Things condition (see Tables A.3-1 and A.3-3). In the original data, the mean number and duration of fixations in *things* AOIs for the Things condition was higher than the number and duration of fixations in *people* AOIs, whereas in the normalized data, the opposite was true, with the mean number and duration of fixations to *people* AOIs being greater than *things* AOIs. However, the mean fixation number and duration for *people* AOIs in the normalized data may be due to the high amount of overlap between *people* and *things* AOIs. Fixations located near the edge of an AOI may have been grouped incorrectly. This would have affected *things* AOIs more than *people* AOIs as *things* AOIs were often located within *people* AOIs, but *people* AOIs were not usually within *things* AOIs. The higher mean

fixation number and duration found in *people* AOIs during the Crosshairs condition in the normalized data further supports this, as again both *things* and *crosshairs* AOIs were often within other AOIs but the *people* AOIs were not.

Overall, both the original and normalization analyses showed that when examining the effects of Condition alone, there was no difference in global fixation numbers or durations between the social (People condition) and non-social domains (Things and Crosshairs conditions). However, there were significant interactions for both fixation measures, demonstrating an influence of interpretation on the distribution of fixation numbers and durations within a scene. While the normalization did eliminate some of the inequalities between the Crosshairs condition and the other conditions, the fixation numbers and durations within *crosshairs* AOIs during the Crosshairs condition remained low, and therefore were likely not due to *crosshairs* AOIs covering less pixel area than other AOIs. Because of this, it was decided that AOI pixel area had little effect on the data and therefore the normalized data was not reported in Chapter 3. Moreover, with pixel area ruled out, it could not be determined if the Crosshairs data was an accurate reflection of participant eye movement during this condition, or if an insufficient ability of the eye tracker to record fixations in these areas, perhaps due to fixations made by participants that were too short to be registered, produced the low fixation counts. Consequently, we made the informed decision to remove the Crosshairs data from further analysis. Only the original eye data to the People and Things conditions (and *people* and *things* AOIs) are reported outside of this section.

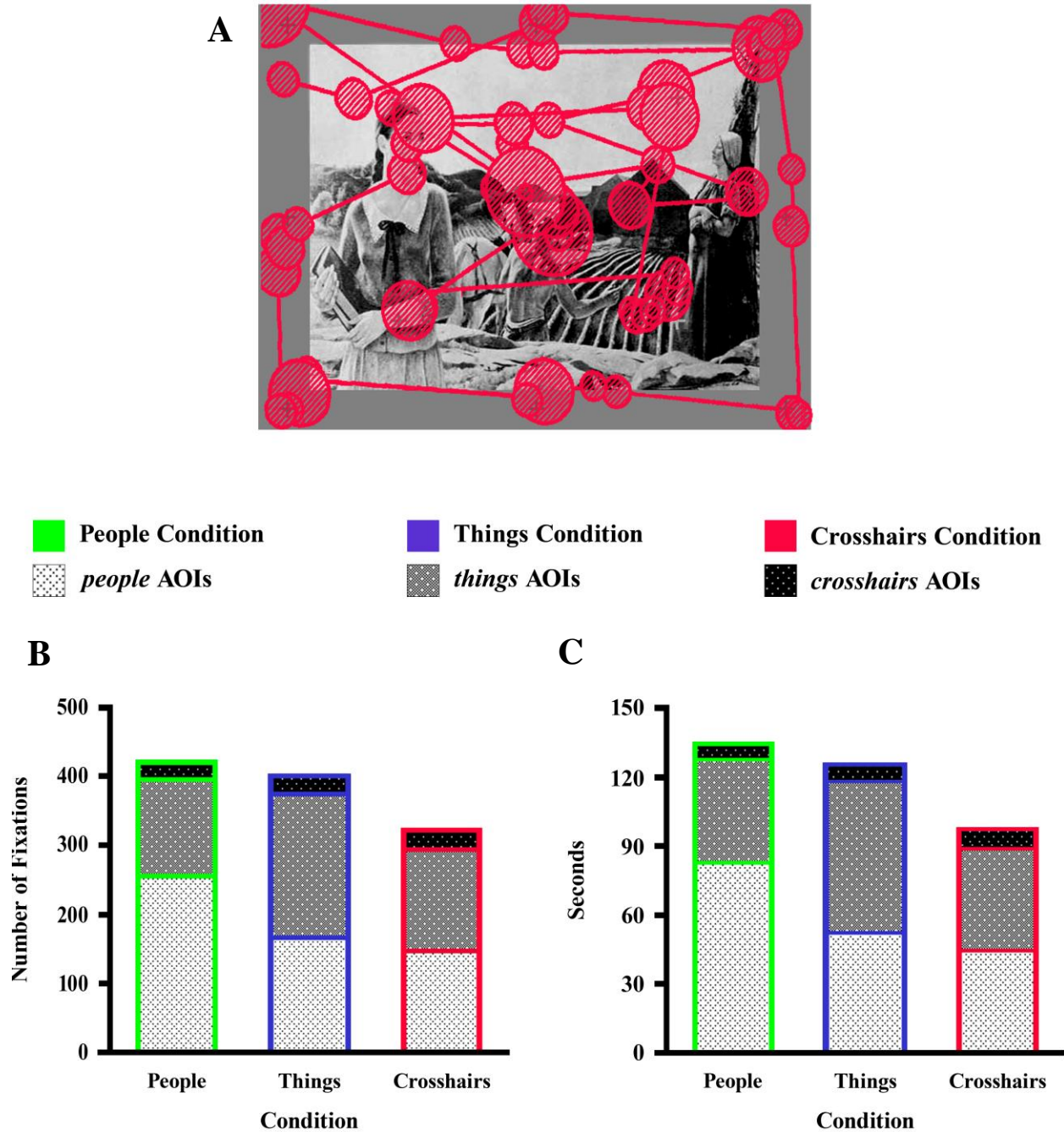
### A.3.8 Figures and Tables



**Figure A.3-1.** Representative outlines for the three AOI categories, with examples of a single *people* AOI in green, a single *things* AOI in blue, and a single *crosshairs* AOI in pink. AOIs were drawn prior to eye movement data analysis, and were not visible to participants during the experiment.

**Table A.3-1. Group means (M) and standard errors (SEs) for original eye movement data**

| Condition  | AOI               | Number of Fixations |           | Fixation Duration |           |
|------------|-------------------|---------------------|-----------|-------------------|-----------|
|            |                   | <i>M</i>            | <i>SE</i> | <i>M</i>          | <i>SE</i> |
| People     | <i>people</i>     | 256.22              | 34.15     | 82324.89          | 11042.68  |
|            | <i>things</i>     | 138.78              | 11.13     | 45139.67          | 3866.67   |
|            | <i>crosshairs</i> | 24.44               | 2.97      | 6671.78           | 726.21    |
| Things     | <i>people</i>     | 166.44              | 20.49     | 51796.33          | 6373.62   |
|            | <i>things</i>     | 207.22              | 17.76     | 66084.33          | 4792.31   |
|            | <i>crosshairs</i> | 26.55               | 4.64      | 7414.11           | 1332.94   |
| Crosshairs | <i>people</i>     | 147.89              | 19.29     | 44234.00          | 6095.56   |
|            | <i>things</i>     | 145.78              | 15.07     | 44093.89          | 4431.77   |
|            | <i>crosshairs</i> | 28.22               | 3.39      | 8519.67           | 1279.65   |



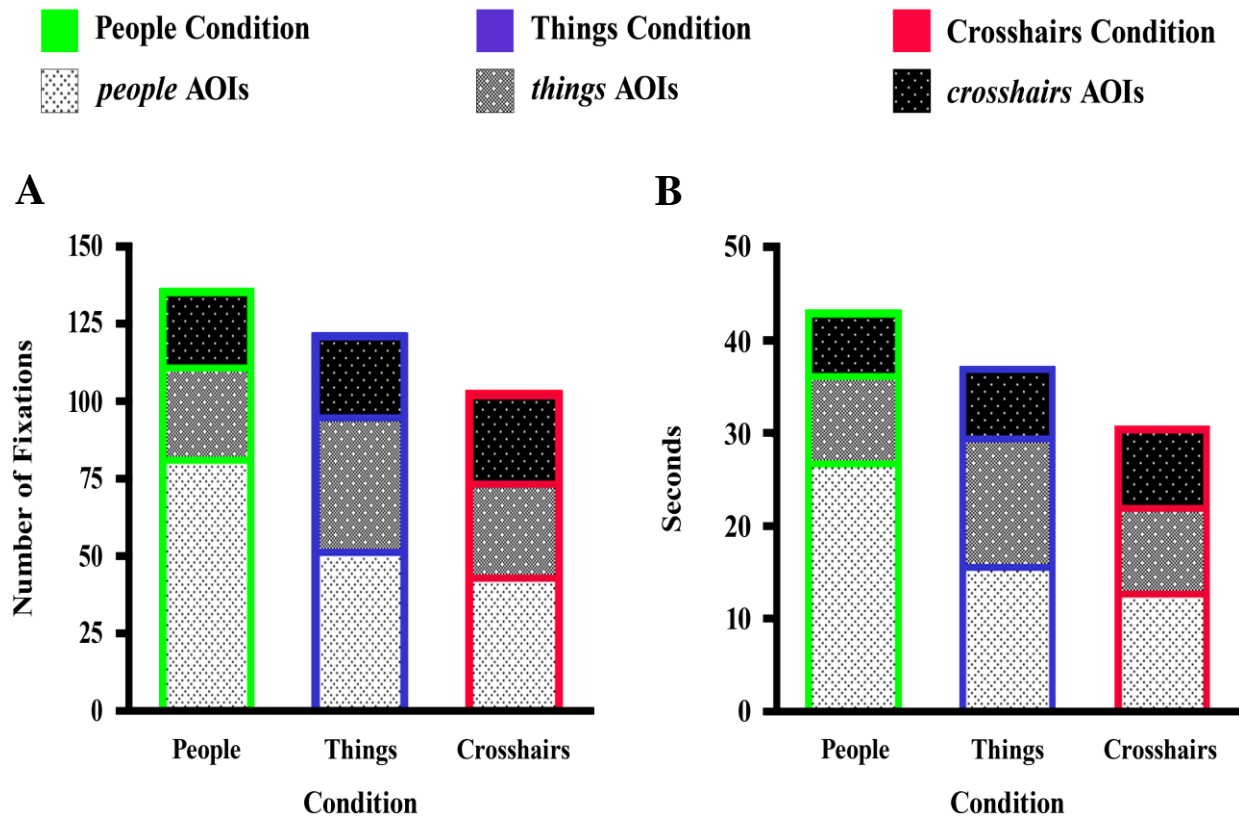
**Figure A.3-2.** Original group fixation data. **A.** Representative single trial fixation pattern for the Crosshairs condition. For fixation patterns to People and Things conditions, see Figure 3-3 in Chapter 3. **B.** Overall mean number of fixations for the three conditions, and the distribution of those fixations across the three AOI categories. **C.** Overall mean fixation duration for each condition in seconds, and the distribution of those durations across the three AOI categories. Colored bars: People condition, green; Things condition, blue; Crosshairs condition, pink. Patterned rectangles: *people* AOIs, white dot pattern; *things* AOIs, grey dot pattern; *crosshairs* AOIs, black dot pattern.

**Table A.3-2. Pixel area measurements as a function of TAT image and AOI category**

| <b>TAT Image</b> | <b>Total Number of Pixels</b> | <b>AOI Category</b> | <b>Number of Pixels in AOI</b> | <b>AOI Pixels / Total Pixels</b> | <b>Adjustment Ratio</b> |
|------------------|-------------------------------|---------------------|--------------------------------|----------------------------------|-------------------------|
| <b>1</b>         | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 62757                          | 0.131                            | 0.636                   |
|                  |                               | <i>things</i>       | 258170                         | 0.538                            | 0.155                   |
| <b>2</b>         | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 90994                          | 0.190                            | 0.439                   |
|                  |                               | <i>things</i>       | 233745                         | 0.487                            | 0.171                   |
| <b>4</b>         | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 242555                         | 0.505                            | 0.165                   |
|                  |                               | <i>things</i>       | 79783                          | 0.166                            | 0.501                   |
| <b>5</b>         | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 61942                          | 0.129                            | 0.645                   |
|                  |                               | <i>things</i>       | 259418                         | 0.540                            | 0.154                   |
| <b>6BM</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 177882                         | 0.371                            | 0.225                   |
|                  |                               | <i>things</i>       | 144195                         | 0.300                            | 0.277                   |
| <b>6GF</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 210673                         | 0.439                            | 0.190                   |
|                  |                               | <i>things</i>       | 118260                         | 0.246                            | 0.338                   |
| <b>7GF</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 139044                         | 0.290                            | 0.287                   |
|                  |                               | <i>things</i>       | 185095                         | 0.386                            | 0.216                   |
| <b>8BM</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 200462                         | 0.418                            | 0.199                   |
|                  |                               | <i>things</i>       | 135753                         | 0.283                            | 0.294                   |
| <b>9GF</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 153468                         | 0.320                            | 0.260                   |
|                  |                               | <i>things</i>       | 165987                         | 0.346                            | 0.241                   |
| <b>12M</b>       | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 179309                         | 0.374                            | 0.223                   |
|                  |                               | <i>things</i>       | 143347                         | 0.299                            | 0.279                   |
| <b>13MF</b>      | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 89834                          | 0.187                            | 0.445                   |
|                  |                               | <i>things</i>       | 232863                         | 0.485                            | 0.171                   |
| <b>15</b>        | 480000                        | <i>crosshairs</i>   | 39936                          | 0.083                            | 1                       |
|                  |                               | <i>people</i>       | 60159                          | 0.125                            | 0.664                   |
|                  |                               | <i>things</i>       | 260128                         | 0.542                            | 0.154                   |

**Table A.3-3. Group means (M) and standard errors (SEs) for normalized eye movement data**

| Condition  | AOI               | Number of Fixations |           | Fixation Duration |           |
|------------|-------------------|---------------------|-----------|-------------------|-----------|
|            |                   | <i>M</i>            | <i>SE</i> | <i>M</i>          | <i>SE</i> |
| People     | <i>people</i>     | 81.11               | 11.73     | 26626.11          | 4042.14   |
|            | <i>things</i>     | 29.50               | 2.46      | 9527.50           | 853.01    |
|            | <i>crosshairs</i> | 24.44               | 2.97      | 6671.78           | 726.21    |
| Things     | <i>people</i>     | 51.05               | 6.10      | 15522.78          | 1878.25   |
|            | <i>things</i>     | 43.52               | 3.63      | 13877.99          | 1063.03   |
|            | <i>crosshairs</i> | 26.55               | 4.64      | 7414.11           | 1332.94   |
| Crosshairs | <i>people</i>     | 42.67               | 5.29      | 12571.72          | 1711.92   |
|            | <i>things</i>     | 30.79               | 3.39      | 9223.08           | 978.74    |
|            | <i>crosshairs</i> | 28.22               | 3.39      | 8519.67           | 1279.65   |



**Figure A.3-3.** Graphs displaying group fixation data that has been normalized for AOI pixel area. **A.** Overall mean number of fixations for the three conditions (colored bars: People condition, green; Things condition, blue; Crosshairs condition, pink), and the distribution of those fixations across each of the three AOI categories (patterned rectangles: *people* AOIs, white dot pattern; *things* AOIs, grey dot pattern; *crosshairs* AOIs, black dot pattern). **B.** Overall mean fixation duration for each condition in seconds (colored bars), and the distribution of those durations across the three AOI categories (patterned rectangles).



## **A.4 fMRI Data to the Crosshairs Condition**

As mentioned in Chapter 4, fMRI data to a third condition (Crosshairs) was collected. The next sections report and discuss the results of the original analysis of the fMRI data for all three conditions with a focus on the response to the Crosshairs condition. Only a brief overview of the task and instructions to participants, along with the fMRI data analysis parameters will be presented here since much of the relevant methodology has already been presented (see Chapter 4).

### **A.4.1 Methods**

Participants were presented with the same set of 12 TAT images that had been overlaid with a 13-crosshair grid (see Appendix Section A.2). The activation task consisted of an event-related design spanning three experimental runs. A single trial began with one of the three word cues presented centrally for 3 s. After a 3 s blank grey screen, one of the 12 manipulated TAT images was presented for 20 s, followed by a 6 s blank grey screen which ended the trial. Overall, there were a total of 36 trials (the 36 word cue / manipulated TAT image pairs) with 12 trials per condition. Trials were divided into three counterbalanced runs so that each manipulated TAT image was shown only once per run. The order in which word cue / manipulated TAT image pairs were presented across the three runs was randomized.

For the imaging run, participants were informed that each scene would remain on the screen for 20 s, during which time they were to visually investigate the image according to the preceding word cue. For the ‘People’ condition, participants were instructed to visually explore the image and mentally construct events relating specifically to the people depicted in each scene. For the ‘Things’ condition, participants were to focus on the non-human items in the scene (e.g., book, violin) as the basis for creating mental scenarios involving the (inanimate) object. In the ‘Crosshairs’ condition, participants were to selectively gaze to and attend the 13 crosshairs in no particular sequence, and disregard the other aspects of the image.

Whole brain axial volumes of BOLD activity were acquired using an eight-channel headcoil in a 3 Tesla GE Horizon LX MRI scanner (GE Medical Systems, Milwaukee, WI, USA). Reconstructed fMRI data were analyzed using AFNI software (<http://afni.nimh.nih.gov/>) and related plug-ins (Cox, 1996), and all anatomical and functional imaging data were

transformed into standardized Talairach coordinate space (Talairach and Tournoux, 1988). In this analysis, group functional data had an individual voxel probability threshold of  $p < 0.01$  and a cluster size minimum of 99 voxels, yielding a whole brain correction with a significance level of  $\alpha < 0.05$  (AFNI plug-in AlphaSim).

#### **A.4.2 Results**

Using a whole brain analysis, we identified group-averaged activation differences in the BOLD responses to each condition and performed contrasts between each set of conditions (six total contrasts). Then conjunction analyses between all three conditions were carried out. The data in this section is therefore broken up into two subsections. The first section describes the results from analyzing the six contrasts between conditions. In the second section, results of the conjunction analyses are presented.

##### ***A.4.2a Contrasts between Conditions***

Activation to People: The only cluster of activation in the People > Things contrast had its center of mass located in the right superior temporal cortex. The People > Crosshairs contrast had clusters of activation centered on the right and left superior and middle temporal gyri as well as clusters in left frontal areas. Group activation to the individual contrasts between the People and Things conditions and the People and Crosshairs conditions are displayed on a template brain in Figure A.4-1. Table A.4-1 lists the anatomical location (center of mass) and number of voxels for each cluster of activation in the contrasts.

Activation to Things: Large clusters of activation in the Things > People contrast were observed in right precuneus and right superior, middle, and inferior frontal cortices. Other areas more active to Things than to People include cingulate gyri, left parahippocampal gyrus, right inferior parietal lobule, and left inferior temporal cortex. The Things > Crosshairs contrast had clusters of activation in middle and inferior occipital cortices and right fusiform. There were also left lateralized responses found in inferior frontal gyrus, lingual gyrus, middle temporal gyrus, and cuneus. Group activation to the individual contrasts between the Things and People conditions and the Things and Crosshairs conditions are displayed on a template brain in Figure A.4-2. Table A.4-2 lists the anatomical location (center of mass) and number of voxels for each cluster of activation in the contrasts.

Activation to Crosshairs: The Crosshairs > People contrast had clusters of activation centered on the precuneus and right superior and inferior frontal gyri as well as clusters in right insula and bilateral middle frontal gyrus. Clusters were also observed in right inferior temporal gyrus, right fusiform, and bilateral thalamus. In the Crosshairs > Things contrast, large clusters of activation were found in right precuneus, bilateral middle frontal gyri, and bilateral postcentral gyri. Additional clusters were identified in bilateral superior frontal gyri, right cingulate, and left lingual gyrus. Group activation to the individual contrasts between the Crosshairs and People conditions and the Crosshairs and Things conditions are displayed on a template brain in Figure A.4-3. Table A.4-3 lists the anatomical location (center of mass) and number of voxels for each cluster of activation in the contrasts.

#### ***A.4.2b Conjunction Analyses***

Activation patterns preferentially activated to each condition were identified using conjunction analyses to determine the overlapping regions in the brain among pairwise contrasts. For pairwise comparisons, group functional data had an individual voxel probability threshold of  $p < 0.01$  and a cluster size minimum of 99 voxels, yielding a whole brain correction with a significance level of  $\alpha < 0.05$  (AFNI plug-in AlphaSim). In the conjunction analyses, only the overlapping clusters of activation between the two pairwise contrasts that were larger than 20 voxels in size were kept.

We first investigated where responses to the People condition were significantly greater than both the Things and Crosshairs conditions. Activity exclusively attributable to People was observed in the right middle temporal gyrus and right superior temporal cortices. The location and size (in number of voxels) of significant clusters of brain activations specific to People ([People > Things] *and* [People > Crosshairs]) are shown displayed on Figure A.4-4 (green), and listed in Table A.4-4.

The conjunction analysis between Things > People *and* Things > Crosshairs identified overlapping activation in these two sets of pairwise contrasts that was specifically related to Things, including bilateral middle occipital cortex, right inferior occipital cortex, right lingual gyrus, left middle frontal gyrus, left inferior frontal gyrus, and a small area of right fusiform gyrus (Figure A.4-4, blue; Table A.4-4).

When the Crosshairs condition was contrasted with both People and Things conditions, a third, more expansive pattern of brain activity was observed (Figure A.4-5, pink). Many regions were activated bilaterally during this condition including precuneus, cuneus, middle frontal gyrus (including the frontal eye fields), postcentral gyrus, cingulate gyrus, superior frontal gyrus, and the inferior and superior parietal lobules. We also observed activation in the medial frontal gyrus, lingual gyrus, right posterior cingulate, and right angular gyrus. The location and size (in number of voxels) of significant clusters of brain activations specific to Crosshairs ([Crosshairs > People] and [Crosshairs > Things]) are shown in Figure A.4-5 (pink) and listed in Table A.4-4.

### **A.4.3 Discussion**

The purpose of this study was to investigate if different interpretations of the same scene would produce differential patterns of activation. Indeed, each of the three interpretation conditions preferentially activated different brain regions. The socially relevant People condition activated regions of the superior temporal cortex, while the non-social Things condition demonstrated activity in regions of inferior temporal cortex and the fusiform gyrus. The activation pattern for People is consistent with previous studies using isolated presentations of social stimuli such as faces and bodies (e.g. Puce et al., 1996; Kanwisher et al., 1997; van de Riet et al., 2009). Activation during the Things condition is similar to previous reports using isolated presentations of objects (e.g. Kohler et al., 1995; Malach et al., 1995; Martin et al., 1995; Martin et al., 1996; Aguirre et al., 1998; Ishai et al., 1999).

The other non-social task, the Crosshairs condition, served as a secondary control (in addition to baseline), allowing for removal of extraneous activity generally related to attention and eye movements, and revealing regions preferentially activated by the other conditions. The robust expanse of brain activity observed for this condition is in line with the role of this condition as an attentional control. The observed Crosshairs-specific pattern of activity spread across frontal and parietal areas. Many of these same areas have previously been linked with eye movement, attention, and working memory processes (see Desimone and Duncan, 1995; Corbetta, 1998; D'Esposito, 2007). For example, the posterior parietal cortices, cuneus, and frontal eye fields have previously been implicated in attentional tasks as being important for preparing and executing voluntary and visually guided saccadic eye movements, as well as for

maintaining an active representation of task-relevant information (Kanwisher and Wojciulik, 2000; Beauchamp et al., 2001; Corbetta and Shulman, 2002; Astafiev et al., 2003; Schendan and Stern, 2007).

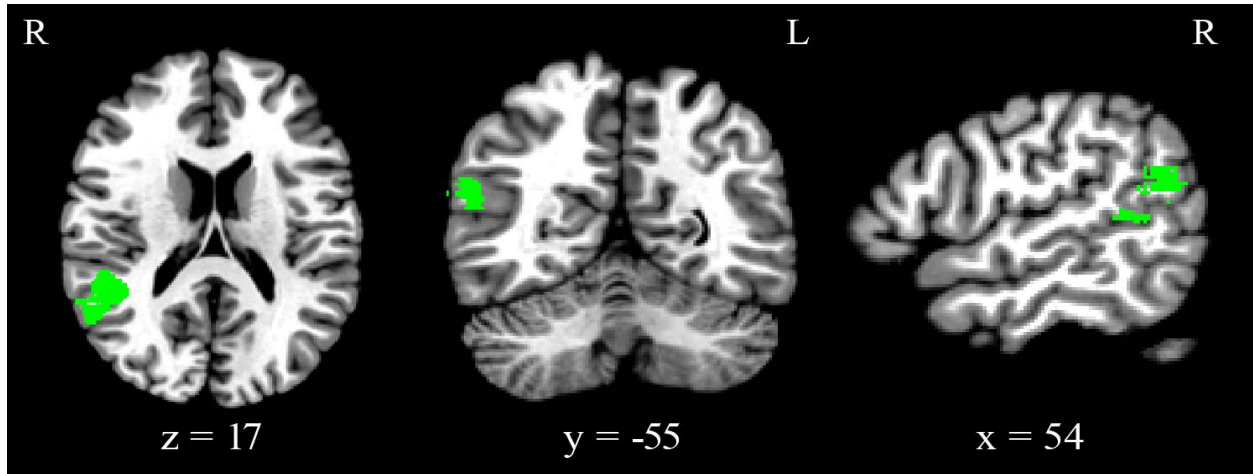
As the Crosshairs condition was the most unnatural of the three conditions, some of the observed activity is potentially the result of participants trying to ignore, via attentional suppression, the elements of the scenes (people, things) that are evolutionarily / developmentally of more interest. Prior research on inhibition demonstrated increased activity in regions of frontal and parietal cortices similar to those found here including, middle and superior frontal gyri, intraparietal sulcus, and cingulate (Garavan et al., 1999; de Zubizaray et al., 2000; Menon et al., 2001; Rubia et al., 2001; Garavan et al., 2002; Horn et al., 2003; Maguire et al., 2003; Mostofsky et al., 2003; Sylvester et al., 2003; Asahi et al., 2004; Fassbender et al., 2004; Kelly et al., 2004; Buchsbaum et al., 2005; Rubia et al., 2005; Wager et al., 2005). Despite the presence of other objects and people, the execution of the Crosshairs task likely inherently limited participants' ability to attend to and process these aspects. A study by Gersch et al. (2004) supports this idea, reporting that the generation of saccade sequences encouraged the dedication of attentional resources primarily to the goal of the next saccade, thus little attention remains available for processing objects at other locations.

However, the unnaturalness of the Crosshairs condition raised several questions and concerns. First, why was the response to this condition so much larger than the brain activation observed during the other two conditions? While attention and working memory likely accounts for some of it, it is hard to interpret the exact reason for such a giant response. It may be that although the eye data suggested participants made less fixations during the Crosshairs condition (Appendix Section A.3), they had to make more eye movements (e.g. saccades) in this condition compared to the other two conditions. While the intention was for Crosshairs to be included as a form of control, and activity was found in eye movement control areas (e.g. frontal eye fields), if participants made *more* movements during this condition, it would no longer be an appropriate control. Rather, the abundance of activity during Crosshairs could be masking areas of activity that might prefer Things or People. Furthermore, the main objective of the study was to determine differences between social and non-social interpretations, which the People and Things conditions sufficiently covered, with little additional information being provided by the Crosshairs condition.

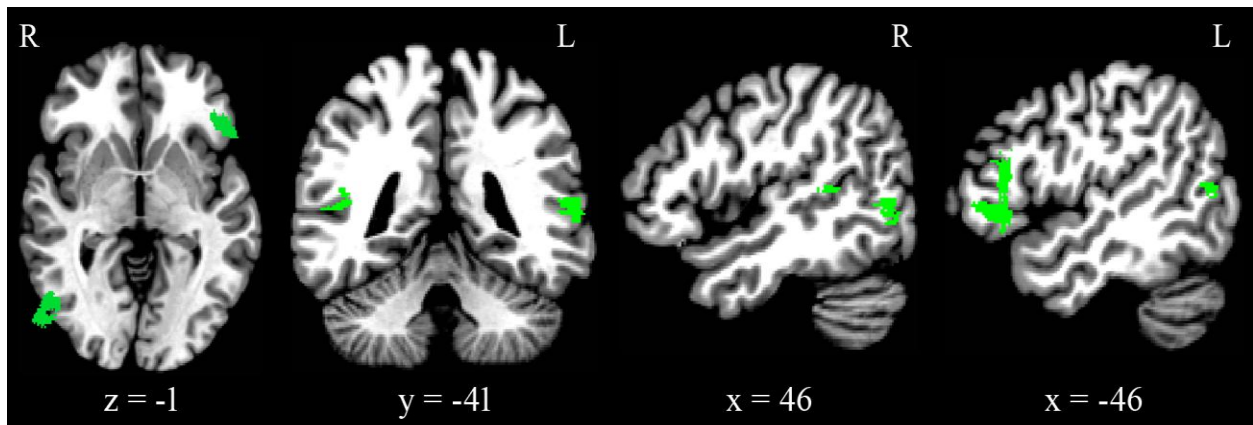
For these reasons, along with the difficulties in interpreting eye data for the Crosshairs condition, it was decided that the crosshairs condition should not be included in subsequent analyses of the fMRI data. The new analysis contrasted the People and Things conditions against the grey blank screen, a stimulus that would adequately control for attention and visual responses without being associated with large eye movement responses. Chapter 4 presents and discusses the results of reanalyzing the fMRI data with the grey screen and without the Crosshairs condition.

#### A.4.4 Figures and Tables

### A People > Things



### B People > Crosshairs



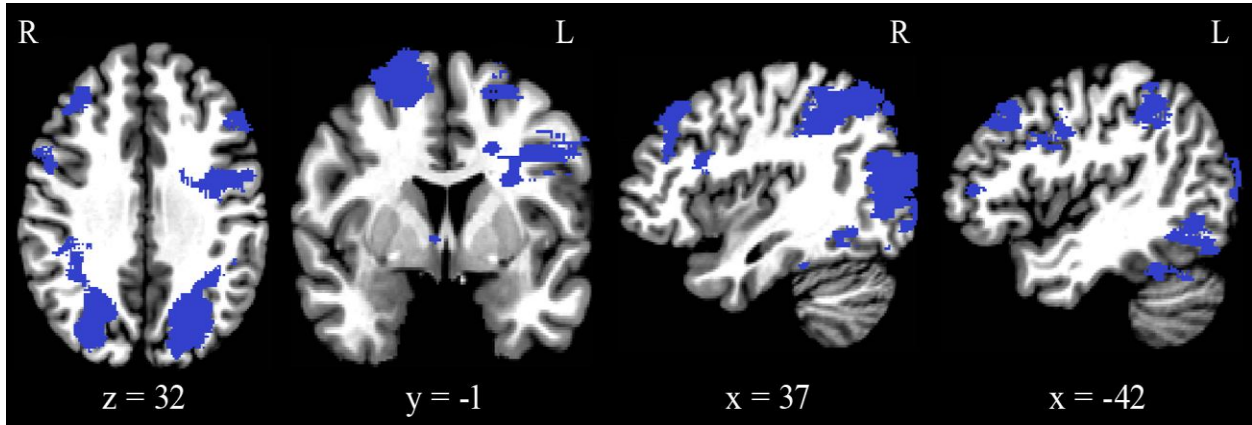
**Figure A.4-1.** Group activation to the People condition ( $p < 0.01$ ,  $\alpha < 0.05$ , cluster-corrected for multiple comparisons). **A.** Regions where activation to People was significantly greater than to Things. **B.** Regions where activation to People was significantly greater than to Crosshairs. Brain activation patterns have been overlaid on a template brain in Talairach space (TT\_N27 Colin brain), with Talairach coordinates (x,y,z) below each slice. R, right; L, Left.

**Table A.4-1. Location and number of activated voxels in the People condition**

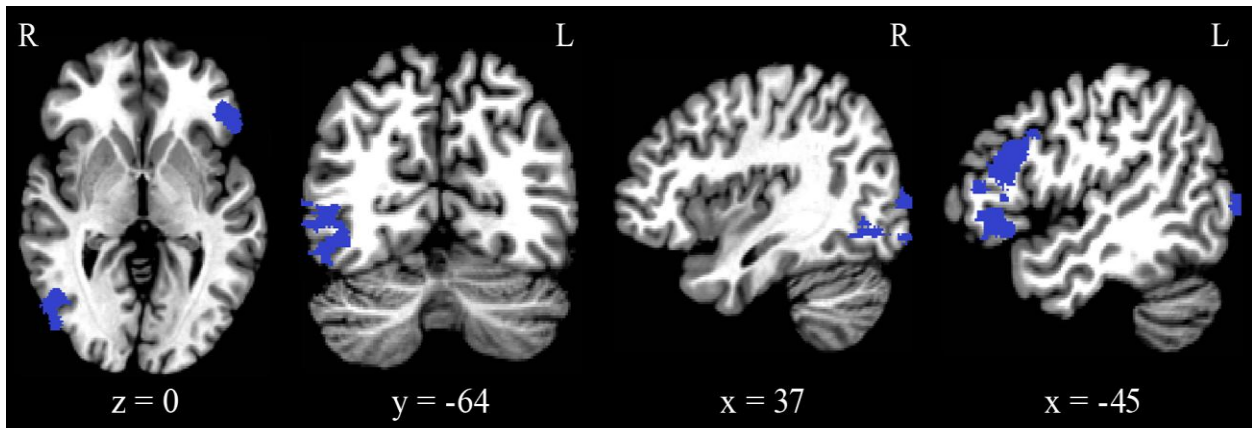
| Anatomical Location           | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|-------------------------------|-------------------------------------|-----|-----|------------------|
|                               | x                                   | y   | z   |                  |
| <i>People &gt; Things</i>     |                                     |     |     |                  |
| Right Superior temporal gyrus | 50                                  | -47 | 16  | 2623             |
| <i>People &gt; Crosshairs</i> |                                     |     |     |                  |
| Left Superior temporal gyrus  | -59                                 | -61 | 16  | 5616             |
| Left Superior frontal gyrus   | -11                                 | 58  | 39  | 4041             |
| Left Inferior frontal gyrus   | -50                                 | 24  | 8   | 2559             |
| Right Middle temporal gyrus   | 56                                  | -62 | 5   | 2010             |
| Right Superior temporal gyrus | 47                                  | -38 | 9   | 243              |
| Left Inferior frontal gyrus   | -37                                 | 27  | -15 | 171              |
| Right Superior temporal gyrus | 64                                  | -51 | 22  | 159              |



### A Things > People



### B Things > Crosshairs

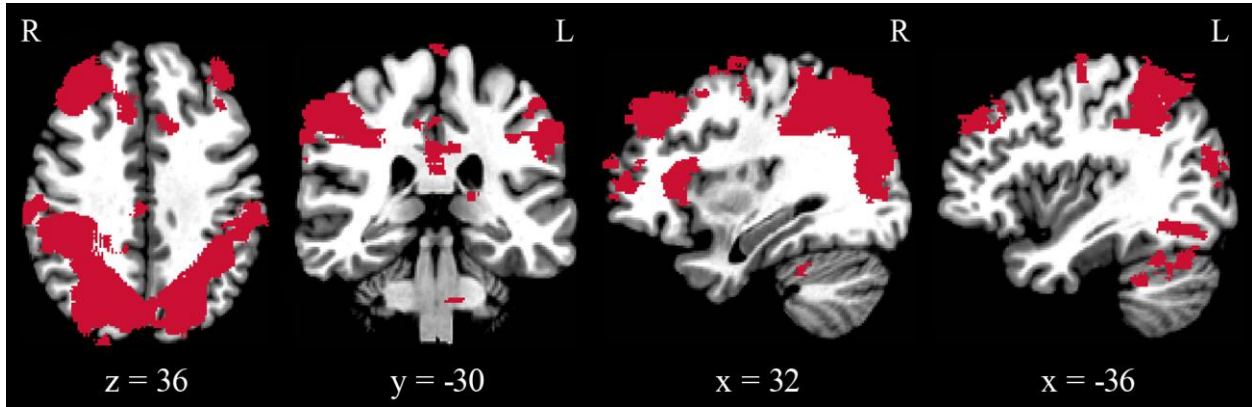


**Figure A.4-2.** Group activation to the Things condition ( $p < 0.01$ ,  $\alpha < 0.05$ , cluster-corrected for multiple comparisons). **A.** Regions where activation to Things was significantly greater than to People. **B.** Regions where activation to Things was significantly greater than to Crosshairs. Brain activation patterns have been overlaid on a template brain in Talairach space (TT\_N27 Colin brain), with Talairach coordinates (x,y,z) below each slice. R, right; L, Left.

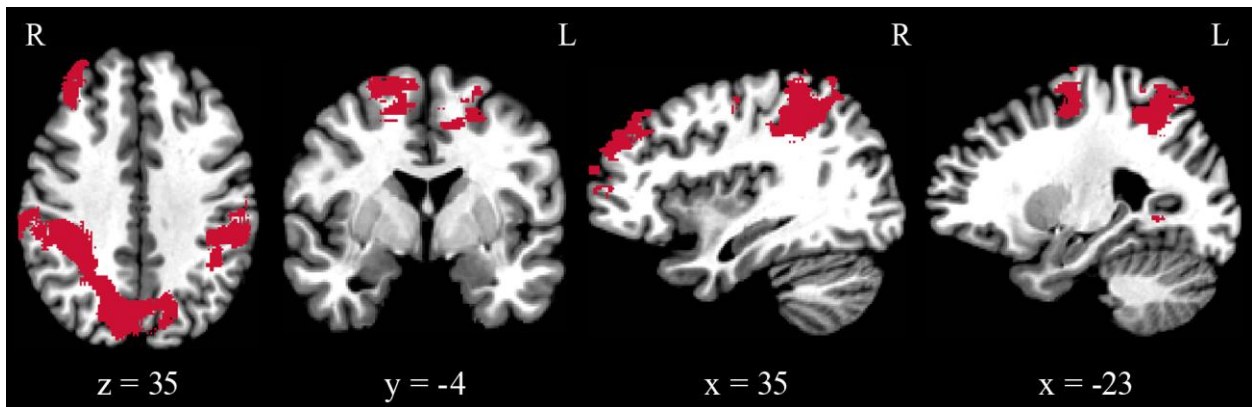
**Table A.4-2. Location and number of activated voxels in the Things condition**

| Anatomical Location            | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|--------------------------------|-------------------------------------|-----|-----|------------------|
|                                | x                                   | y   | z   |                  |
| <i>Things &gt; People</i>      |                                     |     |     |                  |
| Right Precuneus                | 1                                   | -69 | 30  | 117034           |
| Right Middle frontal gyrus     | 33                                  | 34  | 40  | 5540             |
| Right Middle frontal gyrus     | 20                                  | -1  | 61  | 5179             |
| Right Insula                   | 30                                  | 15  | 14  | 4358             |
| Left Inferior frontal gyrus    | -40                                 | 2   | 30  | 3502             |
| Left Middle frontal gyrus      | -28                                 | -7  | 59  | 2611             |
| Left Superior frontal gyrus    | -7                                  | 14  | 48  | 1992             |
| Left Inferior frontal gyrus    | -25                                 | 15  | 6   | 1707             |
| Left Middle frongal gyrus      | -45                                 | 25  | 34  | 1422             |
| Right Cingulate                | 2                                   | -32 | 40  | 1058             |
| Left Middle temporal gyrus     | -69                                 | -39 | -19 | 590              |
| Right Inferior frontal gyrus   | 52                                  | 47  | 5   | 441              |
| Left Middle frontal gyrus      | -40                                 | 40  | 10  | 333              |
| Right Medial frontal gyrus     | 5                                   | -17 | 70  | 330              |
| Right Inferior parietal lobule | 59                                  | -48 | 49  | 325              |
| Left Parahippocampal gyrus     | -31                                 | -23 | -15 | 301              |
| Right Middle frontal gyrus     | 56                                  | 50  | 14  | 274              |
| Left Caudate                   | 0                                   | 9   | 15  | 274              |
| Left Inferior temporal gyrus   | -53                                 | -37 | -16 | 246              |
| Left Cingulate                 | -2                                  | -31 | 26  | 157              |
| Right Middle temporal gyrus    | 58                                  | -42 | -8  | 137              |
| Left Inferior frontal gyrus    | -51                                 | 31  | 17  | 119              |
| Right Middle frontal gyrus     | 48                                  | 39  | 28  | 113              |
| Left Cuneus                    | -20                                 | -96 | 34  | 102              |
| <i>Things &gt; Crosshairs</i>  |                                     |     |     |                  |
| Left Inferior frontal gyrus    | -52                                 | 23  | 9   | 7853             |
| Right Inferior occipital gyrus | 46                                  | -77 | -2  | 6174             |
| Left Middle occipital gyrus    | -35                                 | -92 | 13  | 837              |
| Left Cuneus                    | -25                                 | -99 | -2  | 640              |
| Right Fusiform                 | 20                                  | -95 | -14 | 333              |
| Left Middle occipital gyrus    | -45                                 | -80 | 4   | 321              |
| Left Inferior frontal gyrus    | -39                                 | 28  | -17 | 243              |
| Left Middle temporal gyrus     | -58                                 | -3  | -17 | 186              |
| Left Lingual gyrus             | -23                                 | -87 | -6  | 174              |
| Left Inferior frontal gyrus    | -33                                 | 8   | -12 | 112              |

### A Crosshairs > People



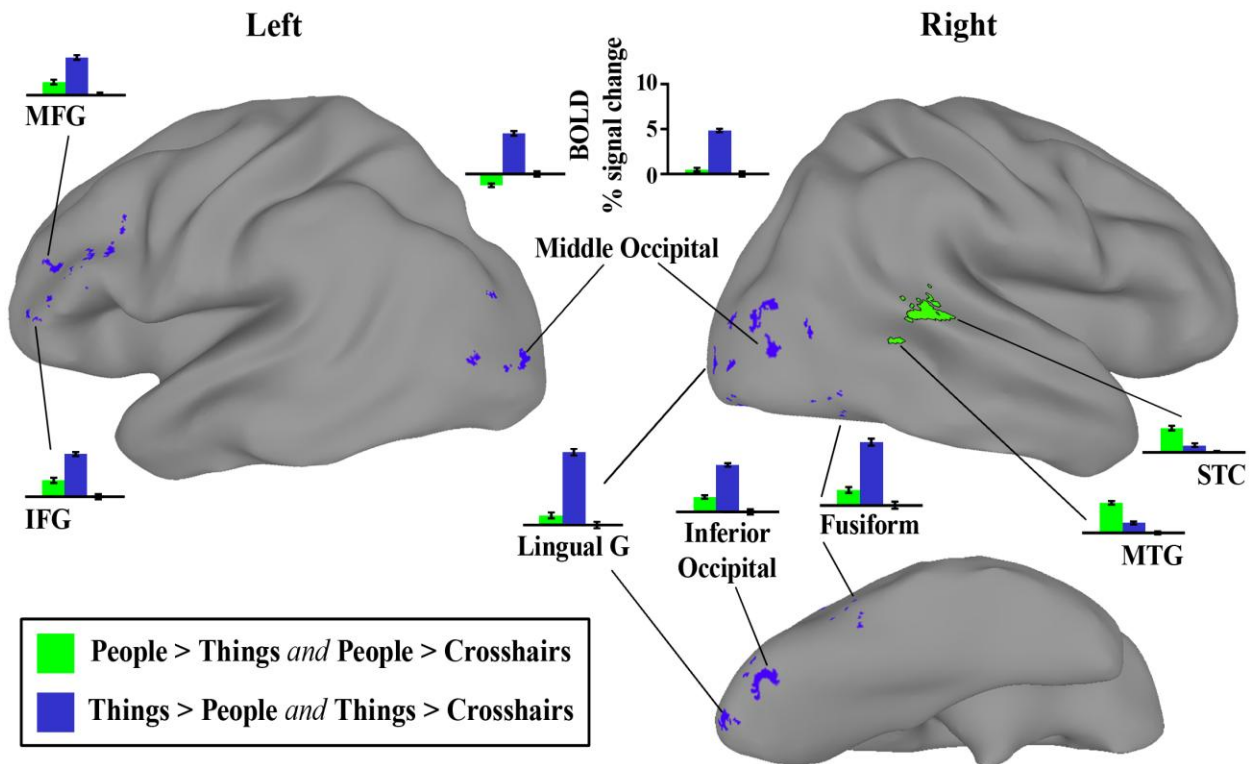
### B Crosshairs > Things



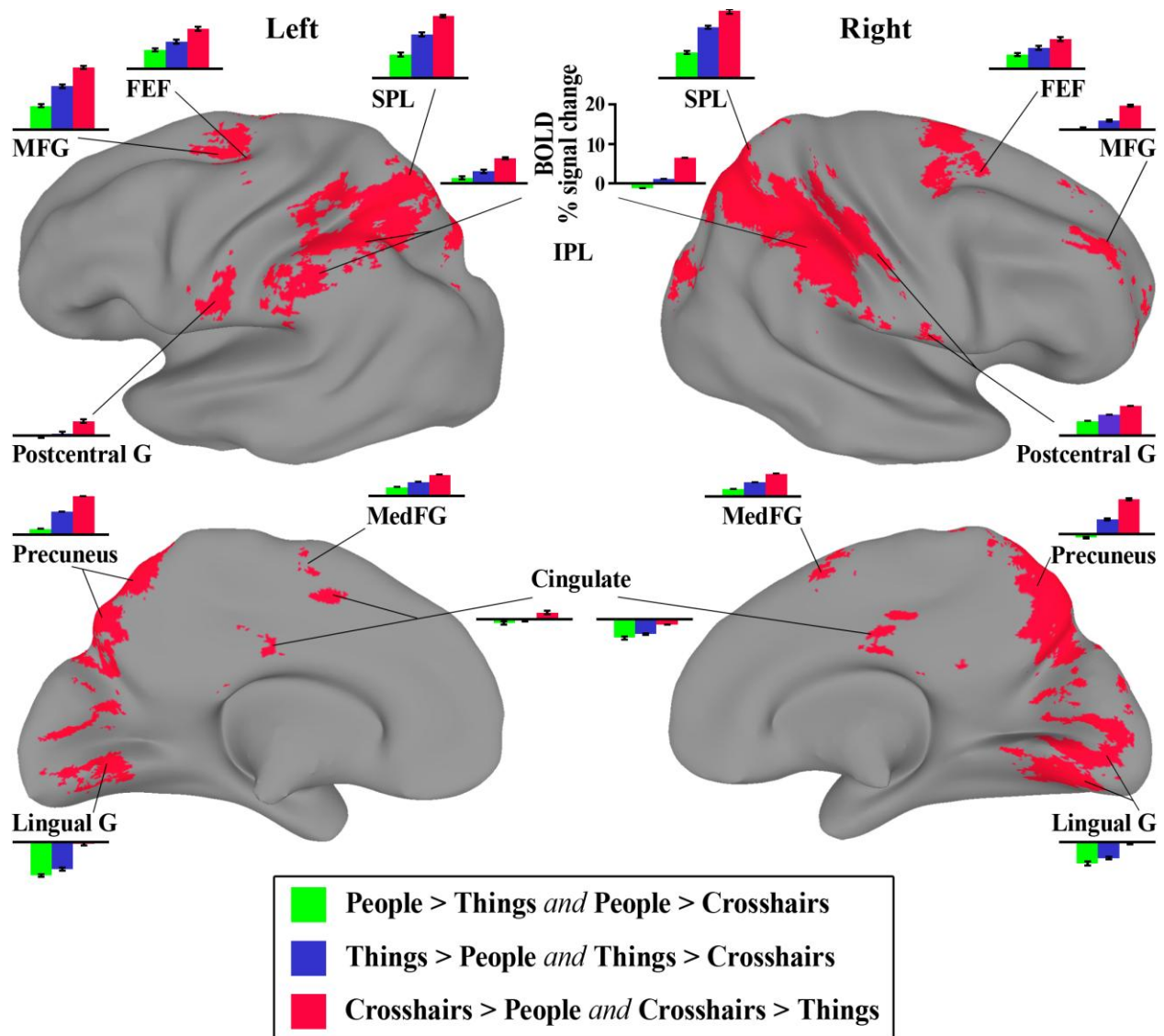
**Figure A.4-3.** Group activation to the Crosshairs condition ( $p < 0.01$ ,  $\alpha < 0.05$ , cluster-corrected for multiple comparisons). **A.** Regions where activation to Crosshairs was significantly greater than to People. **B.** Regions where activation to Crosshairs was significantly greater than to Things. Brain activation patterns have been overlaid on a template brain in Talairach space (TT\_N27 Colin brain), with Talairach coordinates (x,y,z) below each slice. R, right; L, Left.

**Table A.4-3. Location and number of activated voxels in the Crosshairs condition**

| Anatomical Location           | Center of Activation<br>(Talairach) |      |     | Number of Voxels |
|-------------------------------|-------------------------------------|------|-----|------------------|
|                               | x                                   | y    | z   |                  |
| <i>Crosshairs &gt; People</i> |                                     |      |     |                  |
| Precuneus                     | 3                                   | -60  | 40  | 186211           |
| Right Superior frontal gyrus  | 35                                  | 44   | 30  | 18743            |
| Right Insula                  | 28                                  | 22   | 11  | 3472             |
| Left Middle frontal gyrus     | -46                                 | 35   | 34  | 3217             |
| Right Thalamus                | 9                                   | -15  | 7   | 1808             |
| Right Inferior temporal gyrus | 64                                  | -26  | -23 | 1593             |
| Left Thalamus                 | -11                                 | -20  | 8   | 1336             |
| Right Fusiform                | 41                                  | -41  | -24 | 567              |
| Right Inferior temporal gyrus | 55                                  | -50  | -11 | 517              |
| Left Cingulate                | -11                                 | 16   | 37  | 387              |
| Right Postcentral gyrus       | 61                                  | -16  | 20  | 347              |
| Right Superior temporal gyrus | 65                                  | -10  | 2   | 297              |
| Right Precentral gyrus        | 43                                  | -8   | 52  | 257              |
| Right Inferior frontal gyrus  | 51                                  | 9    | 16  | 247              |
| Right Brain stem              | 7                                   | -17  | -17 | 202              |
| Right Cuneus                  | 4                                   | -100 | 29  | 149              |
| Left Cerebellar tonsil        | -10                                 | -33  | -33 | 132              |
| Left Putamen                  | -22                                 | -3   | 8   | 129              |
| Right Middle ftontal gyrus    | 31                                  | 11   | 47  | 118              |
| <i>Crosshairs &gt; People</i> |                                     |      |     |                  |
| Right Precuneus               | 9                                   | -60  | 41  | 77613            |
| Right Middle frontal gyrus    | 20                                  | -4   | 57  | 3790             |
| Right Middle frontal gyrus    | 34                                  | 42   | 34  | 2933             |
| Left Middle frontal gyrus     | -23                                 | -9   | 51  | 2340             |
| Right Middle frontal gyrus    | 33                                  | 51   | 10  | 750              |
| Left Postcentral gyrus        | -57                                 | -23  | 42  | 532              |
| Right Postcentral gyrus       | 42                                  | -43  | 63  | 299              |
| Right Superior frontal gyrus  | 29                                  | 0    | 74  | 244              |
| Right Cingulate               | 3                                   | -23  | 39  | 226              |
| Right Posterior cingulate     | 5                                   | -42  | 24  | 215              |
| Right Middle frontal gyrus    | 34                                  | 56   | 18  | 167              |
| Left Superior frontal gyrus   | -20                                 | -12  | 68  | 121              |
| Left Lingual gyrus            | -21                                 | -56  | -1  | 117              |
| Right Cingulate               | 2                                   | -19  | 30  | 108              |



**Figure A.4-4.** Group brain activation patterns for People and Things conjunction analyses. Activation data illustrating regions where responses to People were significantly greater than both Things and Crosshairs (green), along with regions where responses to Things were significantly greater than People and Crosshairs (blue). Histograms from selected activation clusters depict relative degrees of activation to each condition for each ROI in BOLD percent signal change relative to the Crosshairs condition (mean  $\pm$  standard error). All data are shown projected onto views of inflated brains made using SUMA cortical surface models ( $p < 0.01$ ,  $\alpha < 0.05$ , cluster-corrected). Abbreviations: IFG, inferior frontal gyrus; Lingual G, lingual gyrus; MFG, middle frontal gyrus; MTG, middle temporal gyrus; STC, superior temporal cortex



**Figure A.4-5.** Group brain activation patterns for Crosshairs conjunction analyses. Activation data illustrating regions where responses to Crosshairs were significantly greater than both People *and* Things (pink). Histograms depict relative degrees of activation for each condition within each ROI in BOLD percent signal change (mean  $\pm$  standard error). All data are shown projected onto views of inflated brains made using SUMA cortical surface models ( $p < 0.01$ ,  $\alpha < 0.05$ , cluster-corrected). Abbreviations: FEF, frontal eye field; IPL, inferior parietal lobule; Lingual G, lingual gyrus; MFG, middle frontal gyrus; MedFG, medial frontal gyrus; Postcentral G, postcentral gyrus; SPL, superior parietal lobule

**Table A.4-4. Location and number of activated voxels in conjunction analyses**

| Anatomical Location                         | Center of Activation<br>(Talairach) |     |     | Number of Voxels |
|---|-------------------------------------|-----|-----|------------------|
|   | x                                   | y   | z   |                  |
| People > Things and People > Crosshairs     |                                     |     |     |                  |
| Right Superior temporal gyrus               | 47                                  | -38 | 9   | 111              |
| Right Superior temporal gyrus               | 62                                  | -52 | 21  | 32               |
| Right Middle temporal gyrus                 | 61                                  | -49 | 9   | 31               |
| Right Superior temporal gyrus               | 43                                  | -41 | 15  | 29               |
| Things > People and Things > Crosshairs     |                                     |     |     |                  |
| Right Middle occipital gyrus                | 43                                  | -83 | 8   | 1000             |
| Left Middle occipital gyrus                 | -40                                 | -87 | 17  | 275              |
| Left Middle occipital gyrus                 | -28                                 | -92 | 8   | 143              |
| Right Lingual gyrus                         | 18                                  | -95 | -14 | 104              |
| Left Inferior frontal gyrus                 | -50                                 | 30  | 17  | 61               |
| Right Inferior occipital gyrus              | 30                                  | -85 | -9  | 46               |
| Left Middle frontal gyrus                   | -36                                 | 25  | 21  | 46               |
| Left Inferior frontal gyrus                 | -47                                 | 18  | 21  | 44               |
| Left Inferior frontal gyrus                 | -40                                 | 8   | 30  | 43               |
| Left Inferior frontal gyrus                 | -42                                 | 36  | 10  | 41               |
| Left Middle occipital gyrus                 | -39                                 | -83 | 7   | 37               |
| Left Middle occipital gyrus                 | -31                                 | -85 | 2   | 31               |
| Right Fusiform gyrus                        | 40                                  | -59 | -9  | 28               |
| Left Middle frontal gyrus                   | -46                                 | 14  | 26  | 28               |
| Right Lingual gyrus                         | 27                                  | -86 | -2  | 27               |
| Crosshairs > People and Crosshairs > Things |                                     |     |     |                  |
| Right and Left Precuneus                    | 7                                   | -57 | 39  | 61918            |
| Right Middle frontal gyrus                  | 19                                  | -4  | 56  | 3260             |
| Left Middle frontal gyrus                   | -22                                 | -8  | 51  | 2051             |
| Right Middle frontal gyrus                  | 33                                  | 38  | 38  | 1674             |
| Right Middle frontal gyrus                  | 31                                  | 50  | 10  | 469              |
| Left Postcentral gyrus                      | -55                                 | -24 | 41  | 222              |
| Right Postcentral gyrus                     | 61                                  | -16 | 21  | 206              |
| Right Cingulate gyrus                       | 3                                   | -23 | 39  | 196              |
| Right Superior frontal gyrus                | 34                                  | 56  | 18  | 165              |
| Right Superior frontal gyrus                | 36                                  | 56  | 27  | 125              |
| Left Superior frontal gyrus                 | -19                                 | -12 | 68  | 121              |
| Right Posterior Cingulate gyrus             | 15                                  | -62 | 15  | 117              |
| Right Inferior parietal lobule              | 63                                  | -32 | 25  | 104              |
| Right Postcentral gyrus                     | 3                                   | -48 | 66  | 51               |
| Right Angular gyrus                         | 36                                  | -70 | 32  | 49               |
| Left Cingulate gyrus                        | -7                                  | -17 | 29  | 43               |
| Right Cuneus                                | 26                                  | -76 | 32  | 38               |
| Left Medial frontal gyrus                   | -1                                  | -8  | 59  | 37               |
| Left Superior parietal lobule               | -23                                 | -68 | 59  | 35               |
| Left Lingual gyrus                          | -20                                 | -59 | -1  | 31               |
| Left Cuneus                                 | -7                                  | -84 | 20  | 24               |
| Right Superior parietal lobule              | 43                                  | -64 | 50  | 21               |

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## **CURRICULUM VITAE**

## ***Education***

- 2004-2012**     Ph.D. in Neuroscience, West Virginia University, Morgantown, WV  
**2000-2004**     Bachelor of Science in Neuroscience, Allegheny College, Meadville, PA

## ***Research Experience***

- 2004-2012**     **Effects of Social and Non-Social Interpretations of Complex Images on Human Eye Movement and Brain Activation**  
Advisor: Dr. Aina Puce, West Virginia University
- fMRI data collection and analysis in human subjects using AFNI, FSL
  - Pupillometry and gaze monitoring data collection and analysis
  - Programming in Presentation (Neurobehavioral Systems, Inc)
  - Using and programming in Linux
  - Intermediate experience with EEG, TMS
- 2003-2004**     **Effects of fetal tissue grafts in combination with Deprenyl and RhTGF-Beta 2 on unilateral 6-OHDA lesions in male Sprague Dawley rats**  
Advisor: Dr. Jeffrey Cross, Allegheny College
- 6-OHDA unilateral lesions and surgery techniques in rats
  - Brain extraction and perfusion
  - Rat fetal tissue graft implantation

## ***Publications***

- 2012**     Brefczynski-Lewis JA, Donley S, **Prostko AL**, Puce A. Unique Neural Responses for Disliked vs. Liked Personally Familiar Faces. *Social Neuroscience*, submitted.
- 2012**     **Prostko AL**, Hardee JE, Brefczynski-Lewis JA, Lewis JW, Puce A. Different eye gaze patterns and brain activation for social versus non-social interpretations of complex scenes. *NeuroImage*, submitted.

- 2011** Brefczynski-Lewis JA, Berrebi ME, McNeely ME, **Prostko AL**, Puce A. In the blink of an eye: neural responses elicited to viewing the eye blinks of another individual. *Frontiers in Human Neuroscience*, 5: 68.

### ***Conference Abstracts***

- 2008** **Prostko AL**, Hardee JE, Brefczynski-Lewis J, Pollard SE, Puce A. Differential brain activation patterns to interpreting social scenes under different viewing contexts. *SFN Annual Scientific Meeting*. #789.3

Hardee JE, Thompson JC, **Prostko AL**, Brefczynski-Lewis JA, Puce A. Differential amygdala activation to emotional eyes and eyebrows. *SFN Annual Scientific Meeting*. #786.10

### ***Teaching Experience***

- 2009** Coursework: Teaching practicum, coordinator Dr. Mark Paternostro, West Virginia University  
**The neural basis of high-level object vision**
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**Learning and memory**